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Canadian Journal of Fisheries and Aquatic Sciences

Journal canadien des sciences halieutiques et aquatiques

Government of Canada
Fisheries and Oceans

Scientific Information
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Ottawa K1A 0E6

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Pêches et Océans

Direction de l'information
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Design: Ludvic Saleh & Associates, Ottawa

Conception graphique: Ludvic Saleh & Associates, Ottawa

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Canadian Journal of Fisheries and Aquatic Sciences

Journal canadien des sciences halieutiques et aquatiques

Volume 41, No. 12, December 1984 | **Volume 41, nº 12, décembre 1984**

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Recruitment Patterns in Northwest Atlantic Fish Stocks

J. Anthony Koslow

Department of Oceanography, Dalhousie University, Halifax, N.S. B3H 4J1

Koslow, J. A. 1984. Recruitment patterns in northwest Atlantic fish stocks. Can. J. Fish. Aquat. Sci. 41: 1722–1729.

By analysing recruitment time series for 14 stocks of northwest Atlantic fish, I have found consistent positive correlations in recruitment among stocks within such species as cod (*Gadus morhua*), haddock (*Melanogrammus aeglefinus*), and herring (*Clupea harengus*). Significant positive correlations are also often found in recruitment among demersal, offshore-spawning species (cod, haddock, and redfish (*Sebastes* spp.)), and recruitment in these groups tends to be negatively correlated with that of pelagic species, which spawn inshore (herring) or in restricted waters (mackerel (*Scomber scombrus*)). These patterns emerge as well from a principal component (PC) analysis of the recruitment data. Three dominant patterns (PC 1–3) explain 78% of the variance of the data set. I suggest that the spatial extent of these patterns, which span the region from west Greenland to Georges Bank, indicates that large-scale physical forcing, rather than local biological interactions, predominantly regulates recruitment to northwest Atlantic fisheries.

En analysant des séries chronologiques du recrutement pour 14 stocks de poisson de l'Atlantique du nord-ouest, j'ai constaté des corrélations positives constantes du recrutement parmi les espèces comme la morue (*Gadus morhua*), l'aiglefin (*Melanogrammus aeglefinus*) et le hareng (*Clupea harengus*). On trouve également des corrélations positives significatives pour le recrutement chez les poissons démersaux qui pondent au large (morue, aiglefin et sébastes), et le recrutement dans ces groupes a tendance à être en corrélation négative avec celui des espèces pélagiques qui pondent près de la côte (hareng) ou dans des eaux enfermées (maquereau : *Scomber scombrus*). Ces modes apparaissent aussi si l'on fait l'analyse du composant principal (CP) des données de recrutement. Trois modes dominants (CP1–3) expliquent 78% de la variance des ensembles de données. J'estime que l'étendue géographique de ces modes, de l'ouest du groenland jusqu'au banc de Georges, indique que le recrutement des poissons de l'Atlantique du nord-ouest dépend beaucoup plus du déplacement à grande échelle par des contraintes physiques que d'interactions biologiques locales.

Received November 16, 1983
Accepted August 1, 1984
(J7615)

Reçu le 16 novembre 1983
Accepté le 1 août 1984

The search for an understanding of recruitment variability in fish stocks has been a continuing theme of fisheries research since the turn of the century. A source of fundamental uncertainty has been whether recruitment is determined primarily by biological interactions among fish stocks, as assumed by most stock–recruitment (Ricker 1954; Beverton and Holt 1957) and multispecies fishery models (Andersen and Ursin 1977), or by climate, which regulates underlying physical conditions and production at the base of the food chain (Cushing 1980, 1982; Smith and Eppley 1982; Nelson et al. 1977). Recent studies have shown that large-scale climatic processes, such as the El Niño phenomenon, may regulate plankton production over the extent of an ocean current system (Chelton et al. 1982), and in this way affect larval fish production (Smith and Eppley 1982). In other systems, such as the North Sea and northeast Atlantic, climate has been implicated in changes in plankton abundance (Colebrook 1978, 1982; Koslow 1983) and fishery recruitment (Cushing 1980, 1982), but mechanisms remain obscure.

Analysis of recruitment patterns across an oceanographic province may permit one to examine whether fishery recruitment is predominantly regulated through biological interactions or physical forcing. If recruitment is determined primarily by biological interactions, relationships should be evident between recruitment and spawning stock size. Stronger correlations should be found in recruitment among stocks cooccurring within the restricted limits of stock boundaries than among stocks with disjunct distributions. Cooccurring competitors generally should be negatively correlated. On the other hand, if recruitment is regulated primarily by large-scale climatic processes, recruitment among stocks of the same or ecologically related species should be positively correlated over broad spatial scales.

I have addressed this question through an examination of the recruitment time series of 14 northwest Atlantic fish stocks ranging from the Labrador Sea to the Gulf of Maine for which reasonably accurate, continuous, and lengthy records from virtual population analyses could be obtained (Table 1; Fig. 1). The recruitment-at-age data were lagged to the year of spawning, assuming that year-class size is determined during the first year of life. Correlations were performed on the log-transformed data to minimize the influence of exceptional year-classes. The number of independent data points and thereby the degrees of freedom and significance of the correlations were corrected for autocorrelation in the time series following the method of Garrett and Toulany (1981), a modification of Bayley and

TABLE 1. For northwest Atlantic fish, sources for data on stock size and recruitment based upon cohort analysis. Area names follow Northwest Atlantic Fishery Organization designation. See Fig. 1 for location of stocks.

Species	Area	Source
Cod	1	Sv. Aa. Horsted, NAFO SCR Doc. 82/VI/50
Cod	2J3KL	C. A. Bishop and S. Gavaris, NAFO SCR Doc. 82/IX/111
Cod	3NO	C. Bishop and S. Gavaris, CAFSAC Res. Doc. 82/VI/57
Cod	3Ps	C. Bishop and S. Gavaris, CAFSAC Res. Doc. 81/39
Cod	4TVn	M. Sinclair and J. S. Maguire, CAFSAC Res. Doc. 81/41
Cod	4VsW	J. J. Maguire, G. A. Yound, and A. F. Sinclair, CAFSAC Res. Doc. 82/40
Haddock	4VW	D. E. Waldron, CAFSAC Res. Doc. 80/61
Haddock	4X	R. O'Boyle, CAFSAC Res. Doc. 81/24
Haddock	5Z	S. H. Clark, W. J. Overholtz, and R. C. Hennemuth, J. Northw. Atl. Fish. Sci. 3, 1 (1982)
Redfish	4VWX	D. Clay, CAFSAC Res. Doc. 79/41
Mackerel	Northwest Atlantic	J. J. Maguire, CAFSAC Res. Doc. 81/18
Herring	4WX	M. Sinclair and T. D. Iles, CAFSAC Res. Doc. 81/10
Herring	5Z-6, 5Y	D. S. Miller, CAFSAC Res. Doc. 77/6

Hammersley (1946). Patterns within the correlations were examined both by inspection and through a principal component analysis of the correlation matrix.

Results

Although fishery recruitment is typically highly variable, recruitment among stocks within a species was generally broadly similar throughout the northwest Atlantic. Recruitment in all cod (*Gadus morhua*) stocks examined from west Greenland to the Scotian Shelf, with the exception of Gulf of St. Lawrence (4TVn) cod, generally increased in the early 1960s, peaking around 1963, and then declined until approximately 1970 with some evidence of increased recruitment thereafter (Fig. 2). Recruitment to the herring (*Clupea harengus*) stocks of the Gulf of Maine (5Y-6), Georges Bank (5Z), and Nova Scotia (4WX) generally declined from the 1960s to the 1970s, with the exception of a single very large year-class, which occurred in 1970 in all three stocks. The Georges Bank (5Z), southwest Nova Scotia (4X), and Scotian Shelf (4VW) haddock (*Melanogrammus aeglefinus*) exhibit highly variable recruitment, but also considerable synchrony in the timing of exceptionally good (e.g. 1963) and poor year-classes (circa 1970) (Fig. 2).

This apparent coherence is confirmed by correlation analysis of the log-transformed northwest Atlantic recruitment time series (Table 2). Recruitment was generally strongly correlated within each species: all cod stocks except Gulf of St. Lawrence cod (4TVn), the three haddock, and three herring stocks. Some positive correlations were also found between recruitment to cod and both haddock and redfish (*Sebastes* spp.). Recruitment to the mackerel (*Scomber scombrus*) stock was strongly negatively correlated with recruitment to haddock.

The structure of recruitment relationships among northwest Atlantic fish stocks may be further synthesized and the explanatory power of these patterns determined through an eigenvector or principle component (PC) analysis of the recruitment correlation matrix (Table 2). The first three PCs, which had eigenvalues greater than 1, explained 40.3, 28.8, and 9.0% of the variance, respectively, or a combined 78.1% of the variance of the entire recruitment data set.

Plots of the eigenvectors for PC 1–3 against each other permit the underlying recruitment relationships to be seen graphically (Fig. 3). PC 1 separates recruitment between demersal, offshore spawners (cod, haddock, and redfish), and the pelagic species, herring and mackerel (Fig. 3). PC 2 and PC 3 separate recruitment between species within these broad ecological groups: the herring from the mackerel, and the cod from the haddock (Fig. 3).

Although the principal component analysis highlights the relationships between demersal species on the one hand and pelagics on the other, the basis of this grouping is not altogether clear. Cod, haddock, and redfish are demersal as juveniles and adults, but their larval period is spent in the upper water column, much like the larvae of herring and mackerel. Cod, haddock, and redfish share the offshore banks as their spawning habitat, in contrast with mackerel, which are spawned primarily in the Gulf of St. Lawrence, and the herring, which are generally spawned inshore. However, 5Z herring is spawned on Georges Bank, and its recruitment is positively correlated with that of other herring stocks and negatively correlated with gadoid recruitment. There is also no reason to believe that the inner and outer shelf regions respond oppositely to physical forcing. As gadids, cod and haddock are morphologically similar and have ecological affinities, but their ecology is clearly different from that of redfish, which are viviparous and whose larval morphology is quite distinct. Cod, haddock, and redfish might also be considered cold-water species in contrast with mackerel, which prefers warmer temperatures. However, the temperature range of haddock and herring is similar, but recruitment to these species is generally negatively correlated. Furthermore, recruitment to the cod stocks, which have the broadest geographic range, is coherent from west Greenland to the Scotian Shelf. If the recruitment patterns were temperature dependent, one would expect recruitment to the most northerly and southerly stocks to be negatively correlated. A variety of factors may underlie the correlations in recruitment among species, and their relative importance probably cannot be determined at this time. Furthermore, it should be noted that the strongest, most consistent recruitment relationships are found among stocks within species.

Discussion

The strong correlations generally found in recruitment within species and among related species-groups over large spatial scales in the northwest Atlantic point to the predominant influence of large-scale physical forcing. However, the extent to which biological, as opposed to physical, mechanisms may serve to explain the observed recruitment patterns should be further examined.

If biological interactions among these fish stocks played a significant role in their population dynamics, one would expect to find negative relationships among those stocks with overlapping distributions that were potentially competing with one another. However, examining all such instances in the data, there are in fact positive correlations among the potential

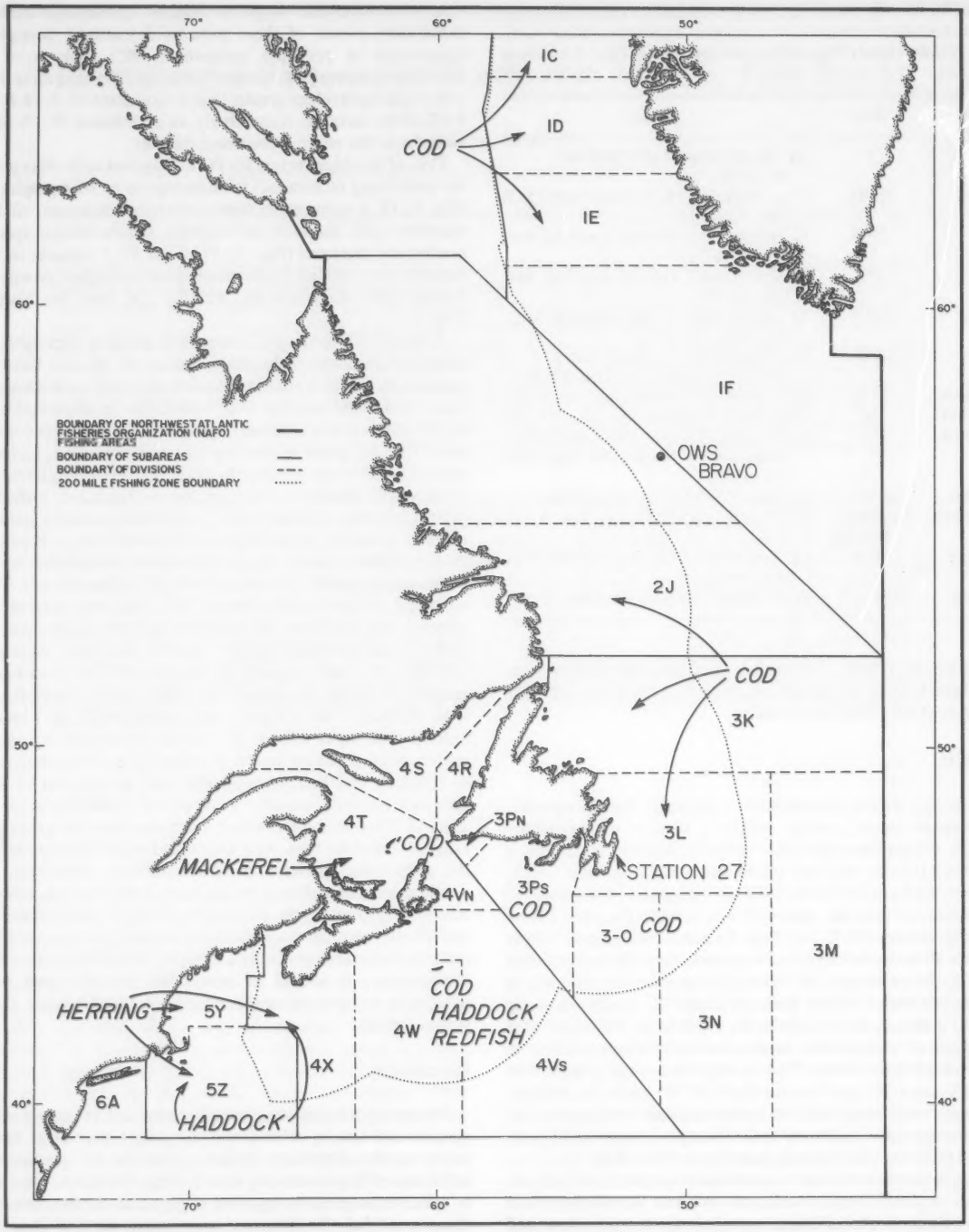

FIG. 1. Northwest Atlantic showing the distribution of fish stocks for which stock and recruitment data were obtained (Table 1), and of station 27 and OWS Bravo on the Labrador Shelf and central Labrador Sea.

TABLE 2. Correlation matrix of log-transformed time series of recruitment to northwest Atlantic fish stocks. Correlation coefficients are given on the right half of the matrix, significance levels on the left. Degrees of freedom and significance levels are corrected for autocorrelation. Locations of the fish stocks: 1, west Greenland; 2J3KL, Labrador Shelf; 3NO, Grand Banks; 3Ps, southern Newfoundland; 4TVn, Gulf of St. Lawrence; 4VW, Scotian Shelf; 4X, southwest Nova Scotia; 5Z6, Georges Bank; 5Y, Gulf of Maine. Significance levels: ?, $p \leq 0.10$; *$p \leq 0.05$; **$p \leq 0.01$; ***$p \leq 0.001$; ns, not significant.

	Cod						Haddock			Redfish,	Mackerel,	Herring		
	1	2J3KL	3NO	3Ps	4TVn	4VsW	4VW	4X	5Z	4VWX	NWATL	4WX	5Z6	5Y
Cod														
1		0.82	0.58	0.72	0.37	0.68	0.54	0.34	0.55	0.62	−0.42	−0.03	−0.20	−0.08
2J3KL	*		0.78	0.58	0.21	0.70	0.73	0.25	0.56	0.68	−0.39	−0.08	−0.02	−0.03
3NO	*	**		0.49	−0.20	0.83	0.65	0.12	0.40	0.76	−0.41	0.33	0.59	0.27
3Ps	**	?	?		0.46	0.59	0.51	0.42	0.38	0.40	−0.52	−0.23	−0.63	−0.36
4TVn	ns	ns	ns	*		0.17	0.26	0.23	0.20	−0.11	−0.25	−0.56	−0.47	−0.15
4VsW	*	*	***	*	ns		0.55	0.04	0.28	0.68	−0.55	0.31	0.51	0.43
Haddock														
4VW	ns	*	*	?	ns	?		0.64	0.82	0.22	−0.80	−0.38	−0.40	−0.25
4X	ns	ns	ns	ns	ns	ns	**		0.78	−0.09	−0.56	−0.71	−0.85	−0.72
5Z	*	*	ns	ns	ns	ns	***	***		0.23	−0.77	−0.17	−0.59	−0.54
Redfish														
4VWX	*	*	**	ns	ns	*	ns	ns	ns		−0.11	0.42	0.34	0.13
Mackerel														
NWATL	ns	ns	ns	ns	ns	ns	**	*	**	ns		0.05	0.12	−0.22
Herring														
4WX	ns	ns	ns	ns	?	ns	ns	*	ns	ns	ns		0.66	0.64
5Z6	ns	ns	?	?	ns	ns	ns	**	?	ns	ns	*		0.77
5Y	ns	ns	ns	ns	ns	ns	ns	*	ns	ns	ns	*	**	

competitors, cod, haddock, and redfish, which cooccur on the Scotian Shelf (4VW). One might also hypothesize that negative correlations should be found in recruitment to stocks forming a predator–prey relationship. However, negative correlations between potential predator–prey pairs (mackerel and 4TVn cod, 5Z haddock and 5Z herring, 4X haddock and 4WX herring) are no stronger than the negative correlations generally found between northwest Atlantic stocks of these species with disjunct distributions (Table 2).

Most of the fish stocks in question were heavily exploited by distant-water fishing fleets and declined during the latter part of the period in question. If recruitment were significantly determined by stock size, regional recruitment patterns might arise as an artifact of common trends in fishing effort and resultant spawning stock size. Therefore, I examined whether there were significant relationships between spawning stock biomass and numbers of recruits.

Time series of spawning stock biomass were available for 11 of the 14 stocks (the exceptions were west Greenland cod, 4VW haddock, and redfish for which data were available only on numbers of spawners, which is not an appropriate index of reproductive effort) (Table 1). Product-moment correlations were again based upon log-transformed data, and the degrees of freedom and significance levels were corrected for autocorrelation as above.

Only 1 of the 11 correlations between stock and recruitment was even marginally significant (herring 5Z: $r = 0.71$; $p = 0.05$). In only one stock could the correlation have been obscured by a second-order relationship. However, the stock–recruit relationship in this case (cod 4TVn) was an inverted dome, the inverse of the expected stock–recruit relationship! I therefore concluded that the observed recruitment relationships were not primarily based upon the overexploitation experienced by many northwest Atlantic stocks during this period. More generally, there is little indication in the data of a significant relationship between recruitment and spawning stock size.

Large-scale physical processes appear most likely to be ultimately responsible for the observed correlations in recruitment among stocks of northwest Atlantic fish. Sutcliffe et al. (1976) have shown that the outflow from the Gulf of St. Lawrence forms an "oceanic pathway" linking the Gulf of St. Lawrence, Scotian Shelf, and Gulf of Maine, such that temperature throughout this region is correlated with discharge levels of the St. Lawrence River. Commercial fish landings in the Gulf of Maine are generally correlated with regional sea surface temperature and the freshwater discharge of the St. Lawrence River (Sutcliffe et al. 1977). Sutcliffe et al. (1983) went on to show that to the north, recruitment of cod on the Labrador Shelf (2J 3KL) was correlated with salinity at station 27 off St. John's, Newfoundland (Fig. 1). Labrador Shelf cod recruitment is negatively correlated with St. Lawrence River outflow as well, which Sutcliffe et al. (1983) used as a surrogate for Hudson Strait freshwater discharge. The relationship appears based upon the strong correlation between salinity and nutrient concentration in the Labrador Current; stratification induced by a low-salinity surface layer also inhibits exchange with the nutrient-rich deeper water (Sutcliffe et al. 1983).

Is the oceanography and fishery recruitment of the northwest Atlantic driven then by common patterns of freshwater discharge? The correlation of cod recruitment in west Greenland, which is under the influence of the west Greenland current, with recruitment to cod stocks along the north American coast argues that large-scale oceanographic influences be examined. Freshwater outflow contributes an estimated 2% of the volume of the Labrador Shelf water, the remainder being composed of water from the Baffin Land current surface water, west Greenland

current, and polar or Baffin Land current subsurface water (Sutcliffe et al. 1983). These water masses mix in the vicinity of Hudson Strait to form the Labrador Current, the main body of which flows south along the 600- to 800-m isobath; the freshwater outflow is largely restricted, however, to the inner shelf (Lazier 1982).

What is the relative importance of the freshwater outflow and of other water masses in regulating salinity and nutrients on the Labrador Shelf? A partial regression analysis was performed on the salinity time series from station 27 (Akenhead 1983) on the Labrador Shelf in relation to St. Lawrence River outflow (Sutcliffe et al. 1976) (used as in Sutcliffe et al. (1983) as a surrogate of Hudson Strait runoff) and salinity at OWS Bravo (Lazier 1980) in the central portion of the Labrador Sea (Fig. 1). The analysis was conducted over the period 1964–74, when data are available from OWS Bravo. River runoff and OWS Bravo salinity were entered into the regression with the lag providing the maximum correlation with station 27 salinity (−3 and +2 mo, respectively). A 3-mo lag seems reasonable for freshwater outflow with station 27, since the maximum flow of the Labrador Current along the slope (0.5–0.8 $m \cdot s^{-1}$) would lead to approximately a 1-mo transit time from Hudson Strait to Grand Banks. Flow along the shelf is somewhat slower, and additional time would be required for the water to pass from the rivers to the mouth of Hudson Bay. The positive lag between salinity at OWS Bravo and station 27 would seem to indicate flow reversal. However, circulation in the central Labrador Sea is sluggish, and the correlations (r) between OWS Bravo and

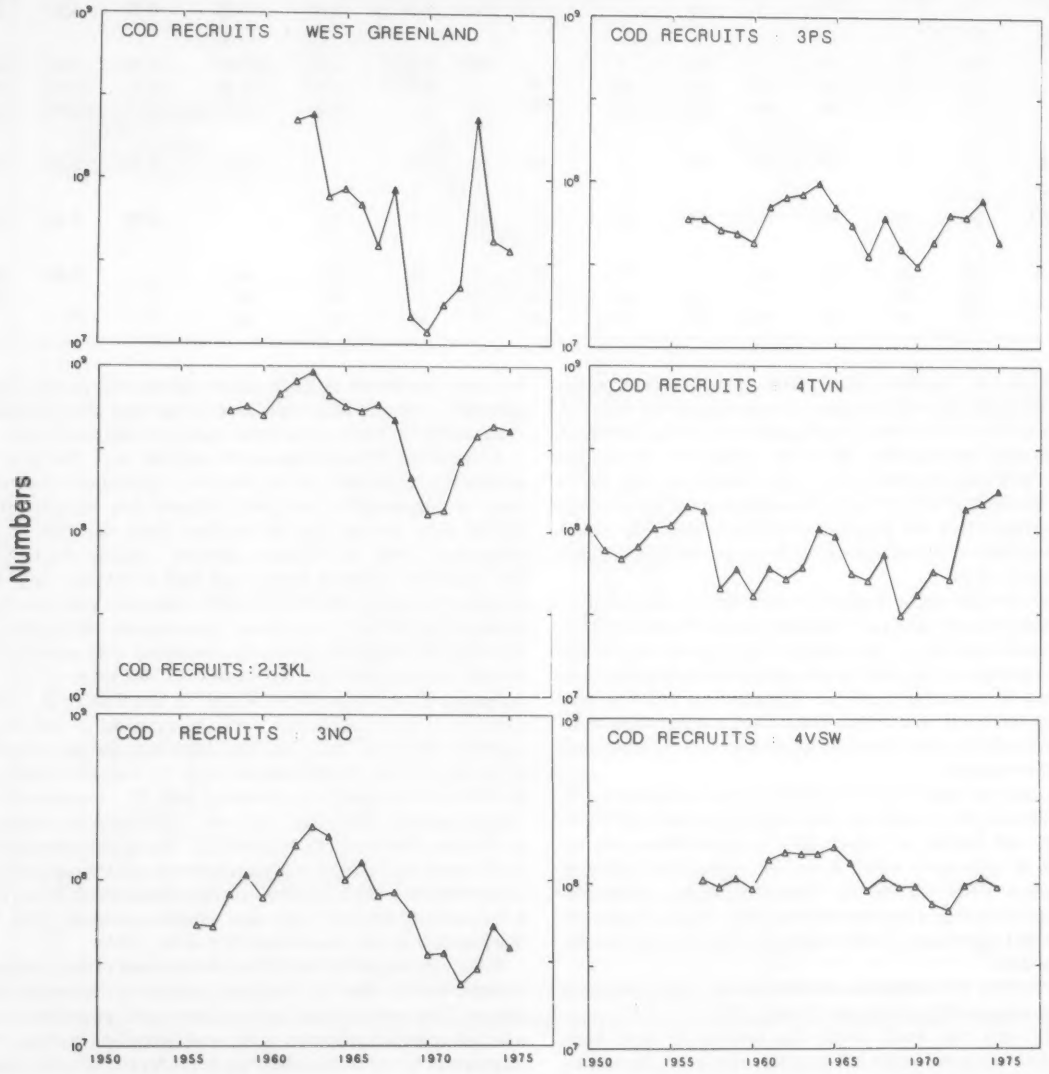

FIG. 2. Time series of numbers of recruits on a log scale lagged back to the year of spawning for 14 northwest Atlantic fish stocks. The time series are from 1950 or the first year for which data from cohort analyses are available (Table 1) and end in 1975. The location of the fish stocks is shown in Fig. 1; the correlation matrix and principal component analysis based upon the recruitment time series are seen in Table 2 and Fig. 3.

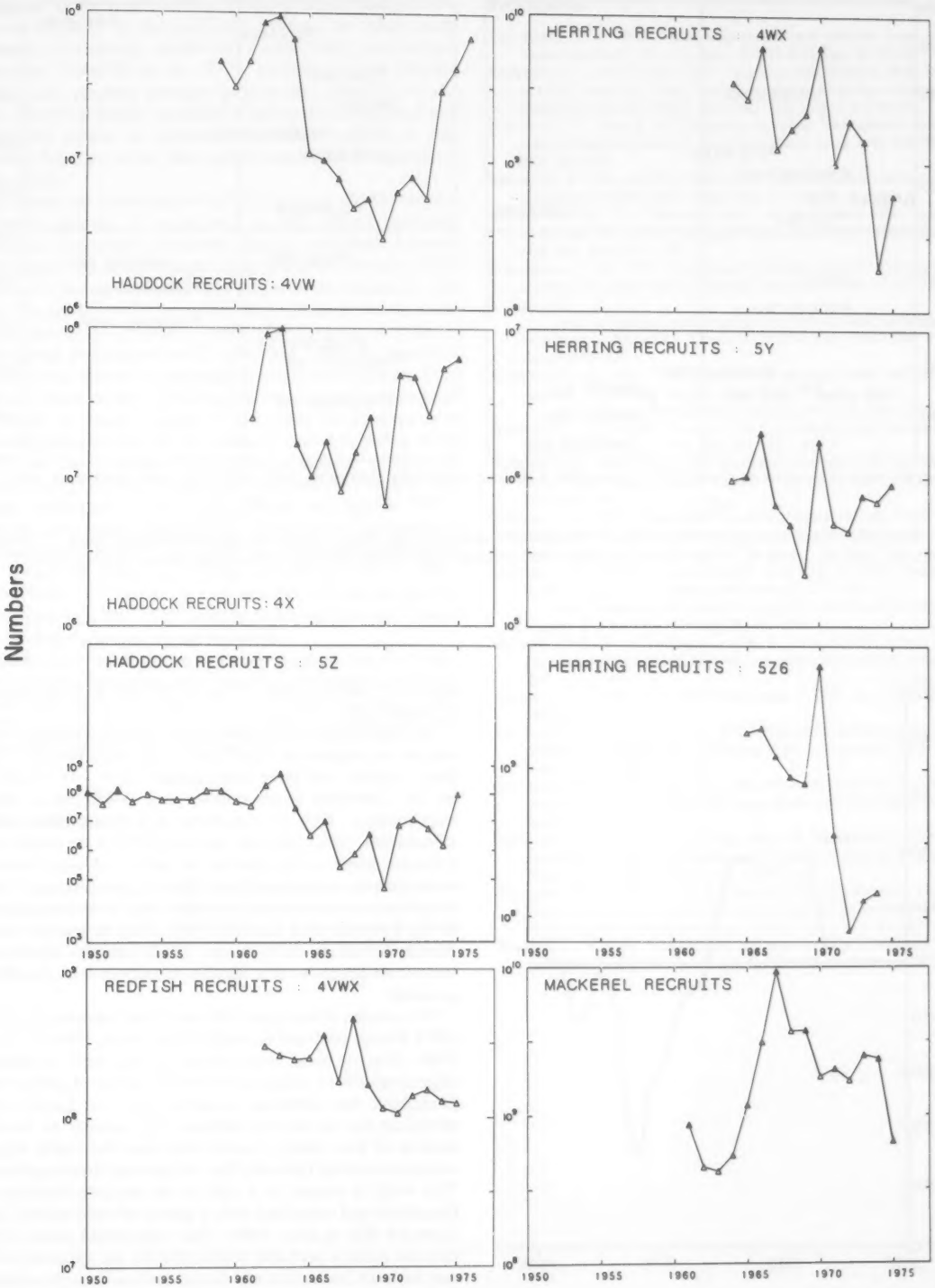

FIG. 2. (*Concluded*)

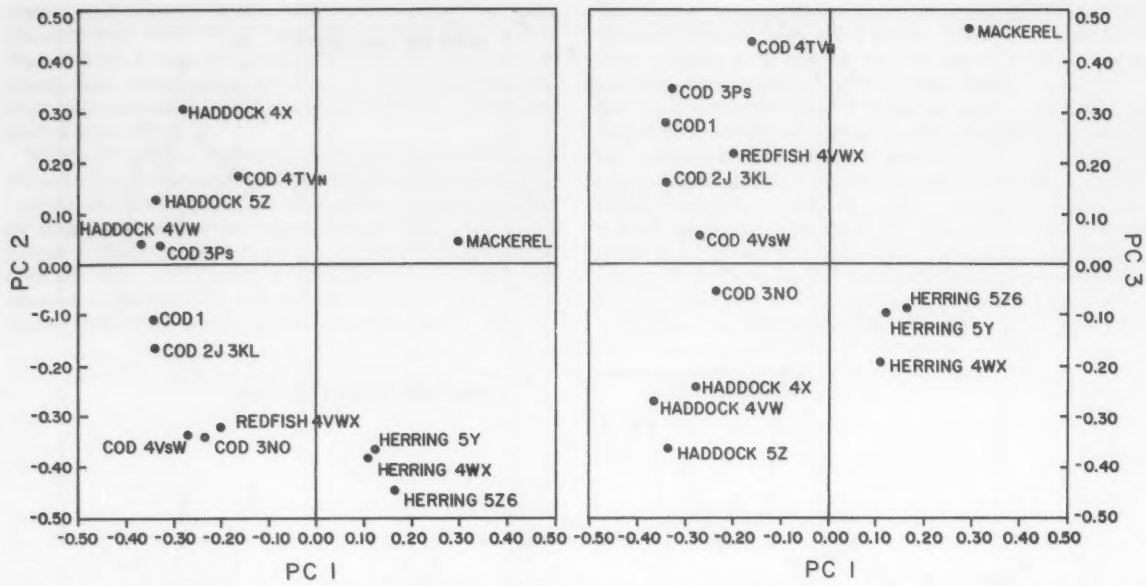

FIG. 3. Plots of the eigenvectors from the principal component (PC) analysis of the fishery recruitment correlation matrix (Table 1). Plots are of PC 1 with PC 2 and PC 1 with PC 3. The relative position of the variables indicates the dominant relationships among them (see text).

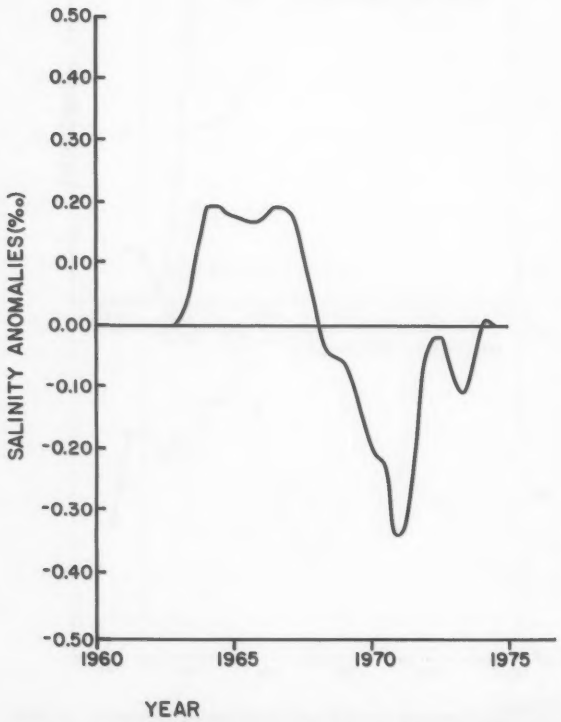

FIG. 4. Twelve-month running mean of surface (0–20 m) salinity anomalies at OWS Bravo, 1964–74.

station 27 salinity with −1 to +2 mo lag only vary between 0.54 and 0.59.

Although both OWS Bravo and St. Lawrence River outflow entered the regression significantly, the contribution of OWS Bravo salinity was three times greater ($B = -0.17$ and 0.51 for St. Lawrence River outflow and OWS Bravo salinity, respectively). This is consistent with water-mass balance calculations, which indicate that over 90% of the nitrate on the Labrador Shelf is supplied by the polar and west Greenland current waters (calculated from Table 1, Sutcliffe et al. 1983), the primary components of the water mass in the central portion of the Labrador Sea (Lazier 1980). Thus it appears that the primary influences upon salinity on the Labrador Shelf are the large-scale processes that regulate salinity in the Labrador Sea generally.

The salinity of the upper 1500 m of the Labrador Sea (i.e. at OWS Bravo) declined throughout the period 1966–71 (Lazier 1980) (Fig. 4) along with salinity on the shelf at station 27 (Akenhead 1983), coincident with the decline of gadoid stocks throughout the northwest Atlantic (Fig. 2). Lazier (1980) attributed the decline in Labrador Sea salinity to increased outflow of low salinity Arctic water into the North Atlantic, which entered the Labrador Sea via the west Greenland current. This event is related to a shift in air pressure blocking over Greenland and coincided with a period of mild winters in the Labrador Sea (Lazier 1980). The widespread nature of this climatic event is probably responsible for the apparent correlation between freshwater and Arctic outflows into the northwest Atlantic.

The apparent relationship between the anomalous winter air pressure blocking over Greenland, the resultant buildup of low salinity water in the Labrador Sea, and the decline in gadoid

recruitment in the mid- to late 1960s is highly suggestive. However, salinity in the northwest Atlantic is linked with large-scale atmospheric conditions (Lazier 1980), sea-surface temperature (Sutcliffe et al. 1977), nutrients, water column stability, and possibly primary productivity (Sutcliffe et al. 1983). There are clearly a number of pathways, both direct and indirect, by which the processes regulating salinity in the Labrador Sea may affect fish recruitment. This area requires further study.

My results are consistent with Templeman's (1972) largely qualitative analysis of recruitment records, which indicated widespread year-class synchrony among northwest Atlantic gadoid stocks. On the other hand, Garrod and Colebrook (1978) performed a principal component analysis of recruitment to fish stocks around the entire rim of the North Atlantic but failed to uncover meaningful patterns. Apparently, large-scale patterns of biological production in the ocean are linked to processes operating over distinct oceanographic or climatic regions. This has been found in the California Current, where zooplankton abundance is closely linked to the trans-Pacific processes regulating advection of the California Current (Chelton et al. 1982), and the abundance of northern anchovy (*Engraulis mordax*) larvae is correlated with zooplankton biomass and primary production in the region (Smith and Eppley 1982). Similarly, long-term changes in the abundance of zooplankton and diatoms in the northeast Atlantic and North Sea seem linked with large-scale physical forcing (Colebrook 1978, 1982; Koslow 1983), as does the recent increase in North Sea gadoid stocks (Cushing 1980, 1982), although the mechanisms responsible for these changes are not yet clear.

Results from these diverse systems suggest that investigations of fishery dynamics and of marine communities generally should focus upon relationships on the ecosystem scale and should examine closely how large-scale oceanographic processes may influence fishery recruitment.

Acknowledgments

This research was supported by grants from the Department of Fisheries and Oceans Subvention program and the Natural Sciences and Engineering Research Council of Canada. S. Marquis assisted with the computer. The manuscript was reviewed by D. Roff and M. Sinclair.

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Variability of Chlorophyll *a* off Southwestern Nova Scotia in Late Fall and Its Relationship to Water Column Stability

R. O. Fournier, R. Ernst, N. B. Hargreaves, M. Van Det, and D. Douglas

Department of Oceanography, Dalhousie University, Halifax, N.S. B3H 4J1

Fournier, R. O., R. Ernst, N. B. Hargreaves, M. Van Det, and D. Douglas. 1984. Variability of chlorophyll *a* off southwestern Nova Scotia in late fall and its relationship to water column stability. Can. J. Fish. Aquat. Sci. 41: 1730–1738.

Chlorophyll *a*, nitrate, and physical variables collected during December 1978 and November 1979 off southwest Nova Scotia show two distinct patterns in phytoplankton abundance. In December 1978, conditions were similar to those expected in late fall over temperate North American shelves. The water was well mixed and chlorophyll was at background level (~0.5 mg/m^3). By contrast, in November 1979, both inshore and offshore regions were stratified, and chlorophyll levels were, in some places, 5 times above background. Two explanations are offered for this bimodal chlorophyll distribution. Offshore, temporary stratification resulted from the intrusion of warm saline water from either the slope or the Gulf of Maine. This may be a temporary condition that eventually deteriorates with seasonal cooling and convective mixing. Inshore, stratification results from the influx of a shallow layer of relatively low-salinity water carried by the Nova Scotia current. The onset and seasonal vagaries of this current help to explain differences observed in 1978 and 1979.

D'après la concentration de la chlorophylle *a*, de nitrate et certaines variables physiques mesurées de décembre 1978 à novembre 1979 au large de la côte sud-ouest de la Nouvelle-Écosse, l'abondance du phytoplancton dans les eaux de cette région suit deux cycles distincts. En décembre 1978, les conditions étaient semblables à ce qu'on peut s'attendre à observer à la fin de l'automne dans la zone tempéré de la plate-forme continentale en Amérique du Nord. Les eaux étaient bien mélangées et la concentration de chlorophylle *a* était au niveau de base (~0,5 mg/m^3). En novembre 1979 par contre, il y avait stratification, tant dans les eaux littorales que dans les eaux du large et à certains endroits la concentration de chlorophylle étaient 5 fois supérieure au niveau de base. On peut donner deux explications à ce changement. La stratification temporaire des eaux du large résulterait de l'arrivée d'eau chaude salée en provenance du talus ou du golfe du Maine. Il se peut que ce phénomène soit temporaire et que la situation se détériore avec le refroidissement saisonnier et le mélange par convection. La stratification des eaux littorales résulte de l'apport d'une couche d'eau peu profonde de salinité relativement faible par le courant de la Nouvelle-Écosse. L'apparition de ce courant et ses mouvements saisonniers peuvent servir à expliquer les différences observées entre 1978 et 1979.

Received September 7, 1983
Accepted August 16, 1984
(J7510)

Reçu le 7 septembre 1983
Accepté le 16 août 1984

The continental shelf off southwestern Nova Scotia possesses relatively high biological abundance (Denman and Herman 1978; Fournier et al. 1984; Smith 1983). The interaction of several physical mechanisms such as tidal mixing (Garrett et al. 1978), upwelling (Garrett and Loucks 1976), and Gulf Stream eddies (Smith 1978; Wroblewski and Cheney 1984) can singly and in various combinations promote favorable conditions for phytoplankton growth. That in turn results in more abundant finfish and shellfish of commercial interest.

Recent biological oceanographic observations in this area have emphasized the summer months when light is abundant and local physical processes work to alleviate nutrient limitation. Fournier et al. (1984) observed a well-mixed inshore region (Fig. 1) which results from the dissipation of tidal energy from currents moving along the coast at velocities of up to 100 cm/s (Garrett et al. 1978). Inshore, chlorophyll concentrations are relatively low (~1.0 mg/m^3) because continuous mixing reduces the average amount of light available to the phytoplankton. Offshore, the well-mixed region merges into a front where stratification increases due to gradients in temperature and salinity. In the frontal zone, reduced mixing permits high nutrients and light to contribute to chlorophyll concentrations of up to 12 mg/m^3 (Fournier et al. 1984). Beyond the front, normal summer conditions prevail, i.e. a highly stratified water column limited renewal of nutrients, and chlorophyll levels fell to between 0.2 and 0.9 mg/m^3. Chlorophyll concentrations have varied from year to year, in all three regions, depending on environmental factors such as cloud cover or local wind mixing.

During summer, an additional mechanism contributes to the observed biological productivity. Coastal upwelling was first inferred (Lauzier 1967) from bottom drifter returns. Garrett and Loucks (1976) later suggested that this 2-cm/s cross-isobath flow was driven by centrifugal forces generated when high-velociity tidal currents turn the corner off southwestern Nova Scotia. Recent current meter observations (Smith 1983) indicate a 3-cm/s cross-shelf flow 10 m off the bottom at the 60-m

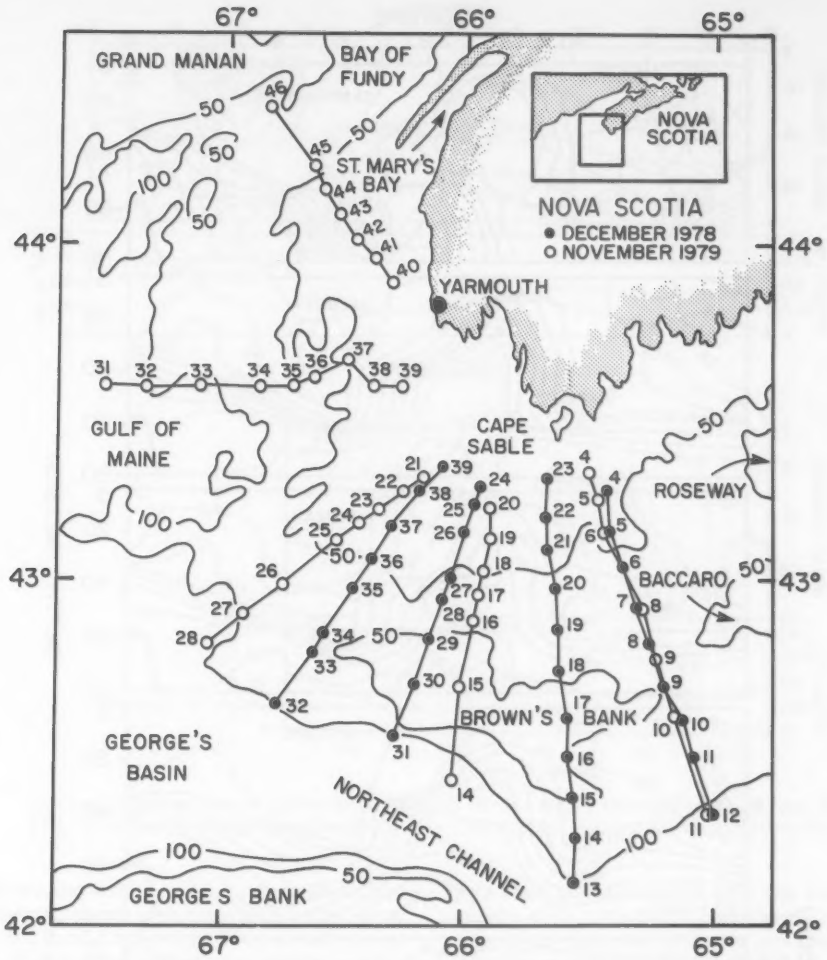

FIG. 1. Shelf region off southwest Nova Scotia from Georges Bank to the mouth of the Bay of Fundy and the stations occupied in December 1978 (●) and November 1979 (○). Depth contours are in fathoms (1 fathom = 1.83 m).

isobath off Cape Sable. However, Smith's work revealed this cross-isobath flow and the resultant upwelling to be seasonal, influenced principally by a dynamic balance between longshore density and pressure gradients. In addition, Smith (1983) has shown that the Nova Scotia current, which is a mixture of inshore Labrador water and freshwater outflow of the St. Lawrence River, has a definite seasonal pattern in transport, a fact previously suggested from geostrophic calculations (Drinkwater et al. 1979; Vermesch et al. 1979). Maximum westward flow occurs in winter with reduction and reversal likely in summer. Winter flow arrives off Cape Sable 5–8 mo (October–January) after freshwater enters the Gulf of St. Lawrence. The salinity or density field off southwest Nova Scotia appears to be controlled principally by local circulation and mixing, but it can also be influenced by the arrival of a seasonal freshwater pulse from the Scotian Shelf. During late fall and winter, bottom cross-isobath flow is greatly reduced or absent, while in summer it is maximum; this is the product of an inverse relationship with a longshore transport.

Summer observations in this area were based on three cruises in July and August when inshore upwelling and the front were most pronounced. Because of this apparent seasonality in the longshore flow, we felt that additional cruises, later in the year, would help to define the phytoplankton response to changing physical conditions. Consequently, this paper describes observations in late fall that aim to identify the physical mechanisms that contribute to the biological uniqueness of the region.

Methods

The study area off southwestern Nova Scotia (Fig.1) was visited on two occasions: the 1978 cruise (12–15 December) consisted of four transects with 29 stations occupied; in 1979 (5–9 November), 46 stations were visited over five transects. The 1979 transects were identical with those reported previously on summer conditions (Fournier et al. 1984).

The sampling routine was similar for all stations. Vertical sampling was carried out using a General Oceanics rosette

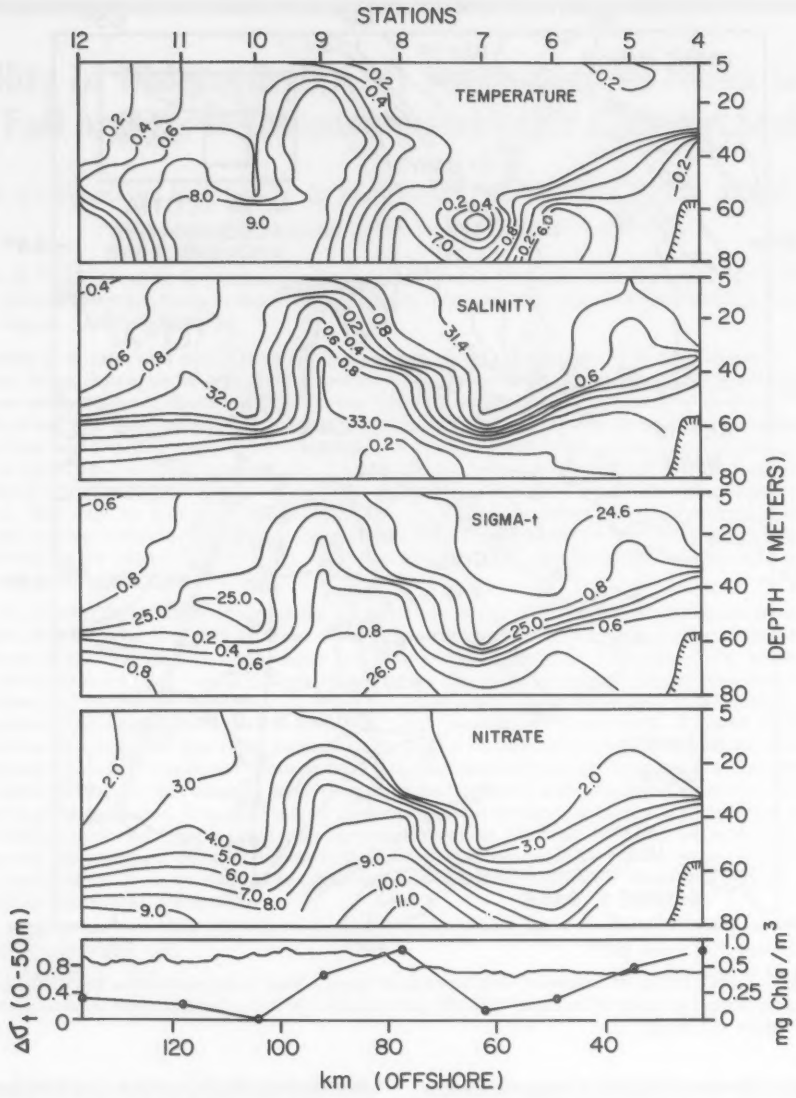

FIG. 2. Vertical profiles of temperature, salinity, sigma-*t*, nitrate, continuous in vivo surface chlorophyll (●—●), and the difference in density between the surface and 50 m (—) for stations 4–12, December 1978.

equipped with ten 5-L Niskin bottles and a Guidline analog C.T.D. sensor. Samples were collected at 10-m intervals to 50 m followed by 25-m intervals to 150 m, depending on the total depth. Analyses were conducted for salinity, chlorophyll, and nitrate. Nutrient analyses were carried out using a Technicon procedure for nitrate (158–71w). Finally, if light permitted, a Secchi disk reading was made.

Between stations, continuous observations of surface fluorescence, temperature, and salinity were made on water pumped through a fitting in the ship's hull from a depth of about 2 m. Fluorescence, measured using a Turner Designs (model 10-000) fluorometer, was later corrected to equivalent chlorophyll concentration using a linear regression produced from calibration water samples, obtained at 0.5-h intervals throughout each cruise. Temperature and salinity were measured using either a deck-mounted guidline C.T.D. or Grundy model 6620 thermosalinograph.

Results

Temperature and salinity varied in a similar fashion off southwest Nova Scotia in December 1978 (Fig. 2 and 3). With the exception of a cool, deep pocket inshore, relatively cool, freshwater (6–9°C, 31.4–33.2‰) extended as a continuous surface layer over the length of the first section (Fig. 2). The resulting sharply defined pycnocline deepened steadily, except for a vertical excursion in midtransect in the vicinity of Browns Bank (stations 8–10), from an inshore low of 40 m to 65 m

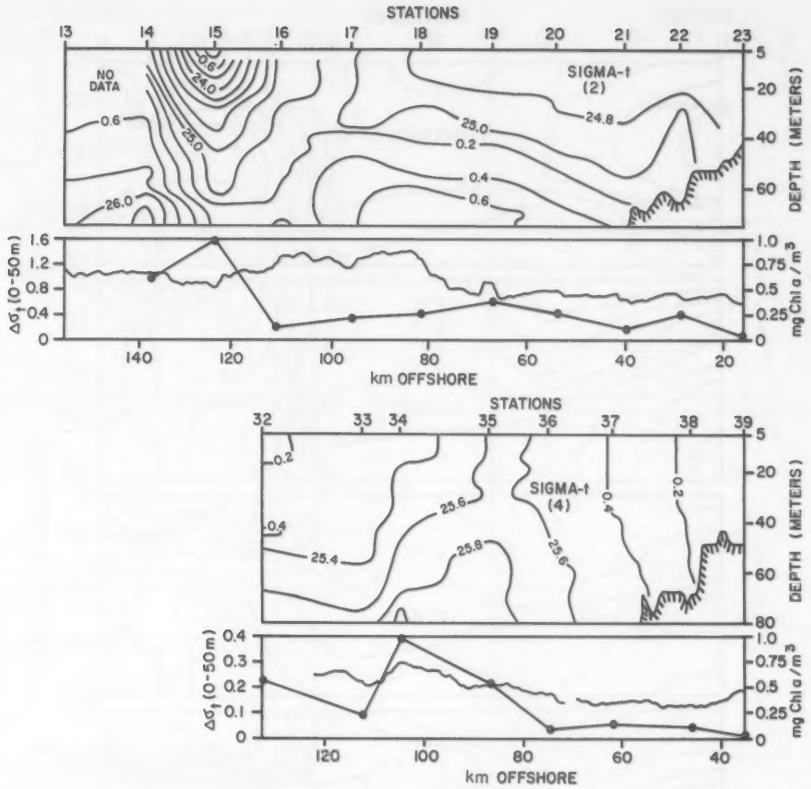

FIG. 3. Vertical profiles of sigma-*t* and continuous in vivo surface chlorophyll (●—●) and the difference in density between the surface and 50 m (—) for stations 13–23 and 32–39, December 1978.

offshore. This density distribution, which is largely determined by the salinity gradient, appears to be responsible for the nitrate distribution (1.5–9.0 μm/L) in the upper 50 m, as well. A continuous chlorophyll trace shows surface concentrations ranging steadily between 0.4 and 0.8 mg/m^3 with no discerable trend visible, even in midtransect where mixing is reduced and nutrients are more abundant.

Transects 2 and 4 (Fig. 3) show progressively more mixing inshore, with passage from east to west. The prominent pycnocline of section 1 is no longer visible, although isopycnals still approach the surface near Browns Bank (stations 16–18 and 34–36). One slight difference is the indication, from the continuous traces, of a slight increase in chlorophyll concentrations with increasing distance offshore. In both cases, a density gradient was associated with the increases. In general, despite some localized, small-scale variability, conditions observed in December 1978 were consistent with seasonal expectations, i.e. a relatively uniform temperature and salinity regime across the shelf, reasonably intense mixing with a pycnocline present at about 50 m, and high nitrate and low chlorophyll throughout the area.

November 1979 data (Fig.4 and 5) show the presence of the Nova Scotia current in the area as a region of strong temperature and salinity gradients (6–11°C, 31.6–33.4‰) extending about 60 km out from the coast. These values are not unlike those observed for the full shelf during the previous December. Inclusion of the offshore ends of each transect would raise the upper limits of the ranges to 13°C and 34.4‰, respectively. Isopleths at the outer end of each transect suggest intrusion of warm saline water into the study area, presumably from the slope. The pronounced, deep, shelf-wide pycnocline, so prominent the previous fall, was not in evidence. Instead, some stratification was observed at each end of both transects, while the midsection was almost completely mixed. Nitrate showed an inverse relationship with mixing, while chlorophyll was highest where stratification was greatest. Consequently, sections 1 and 2 show a bimodal chlorophyll distribution with concentrations falling between 1.0 and 2.5 mg/m^3, as much as 5 times those measured in the same area the previous December.

The remaining section in November (Fig. 6) showed a considerable reduction in vertical stratification. All evidence of low-temperature (<9.0°C) and low-salinity (<32.4‰) water, previously identified with the longshore current, has disappeared. No pycnocline was obvious. Nitrate concentrations were high, showing a decline only where chlorophyll was also high, i.e. at the offshore end of the transect. There, the relatively higher temperatures and salinities, linked earlier to intruding slope water, were still visible. Although data are not present for transects 4 and 5, they showed a continuation of the trend described above. Section 4 was generally well mixed inshore, with some stratification and relatively higher chlorophyll offshore. Section 5, located across the mouth of the Bay of Fundy (Fig. 1), was almost totally mixed over its entire length, from top to bottom. In general, November chlorophyll levels

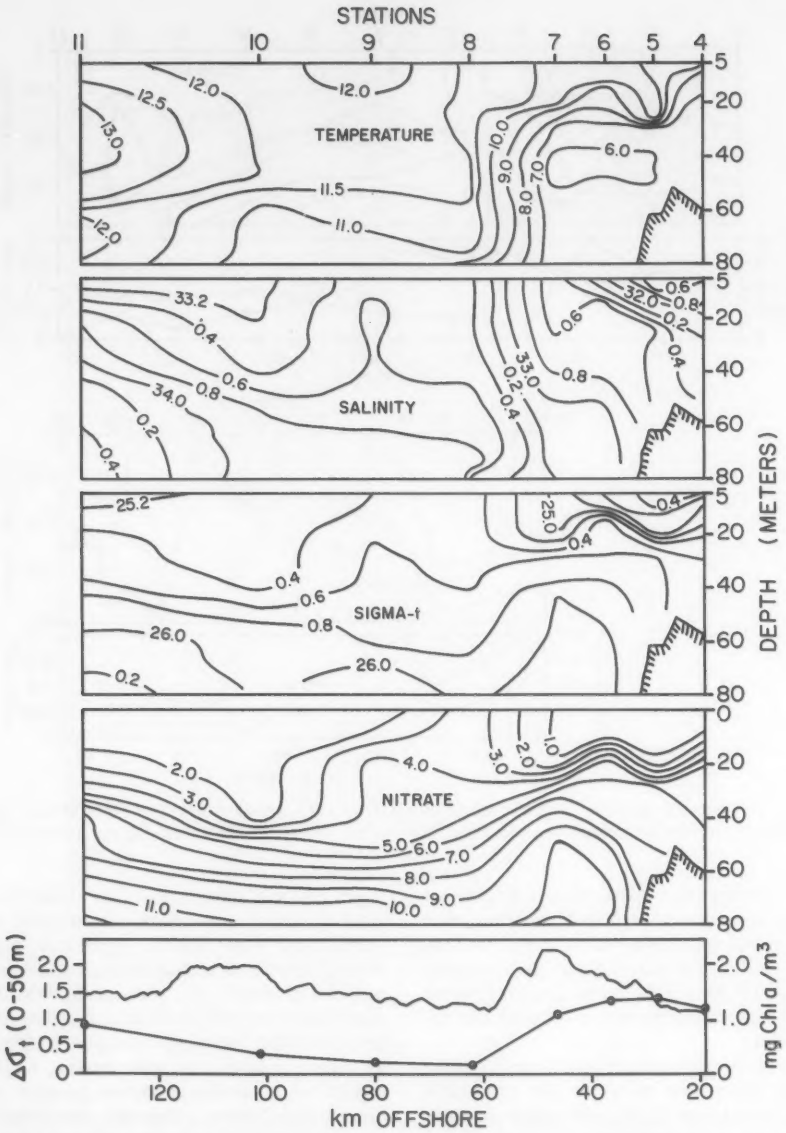

FIG. 4. Vertical profiles of temperature, salinity, sigma-*t*, nitrate, continuous in vivo surface chlorophyll (●—●), and the difference in density between the surface and 50 m (—) for stations 4–11, November 1979.

were higher than expected off southwest Nova Scotia, showing a biomodal distribution at the eastern end of the Gulf of Maine and undistinguished seasonal background levels in the western end.

To compare the physical environments observed on both cruises, the density differences between the surface and 50 m at three inner stations of each transect were averaged and then plotted (Fig. 7). Data from three previous summer cruises (Fournier et al. 1984) were also included to broaden the comparison. With one exception, water column stability was always greatest at the eastern end of the study area, after which it dropped precipitously to the regional low southwest of Cape Sable (Fig. 1). This low, which is consistent with the prediction of Garrett et al. (1978) and the findings of Smith (1983), has been identified as the site where maximum dissipation of tidal energy occurs. Beyond that point, the water column once again came under stabilizing influences. Perhaps the most significant feature of Fig. 7 is the clear demonstration of variability within the first three sections, not only between seasons but within as well. The highest and lowest stratification observed occurred in the November and December data, respectively. This difference is further illustrated by plotting temperature and salinity data

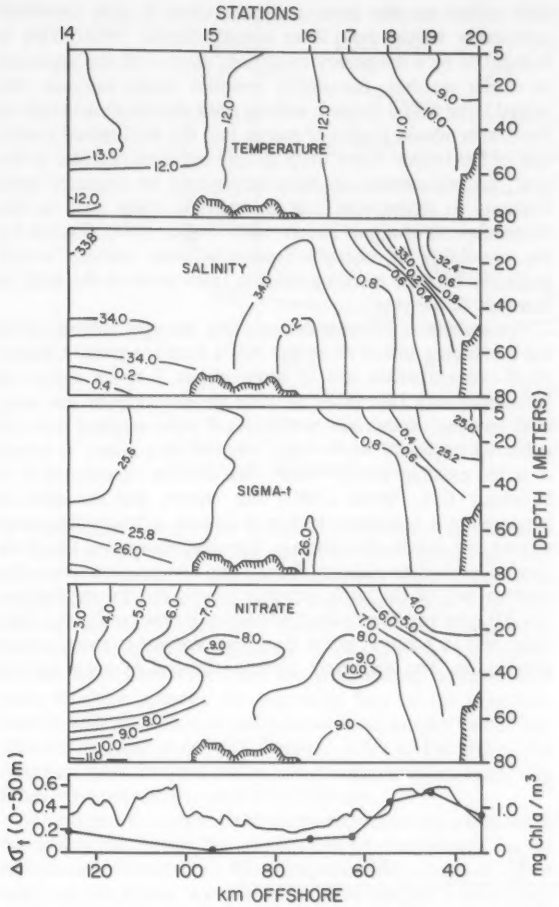

FIG. 5. Vertical profiles of temperature, salinity, sigma-*t*, nitrate, continuous in vivo surface chlorophyll (●—●), and the difference in density between the surface and 50 m (—) for stations 14–20, November 1979.

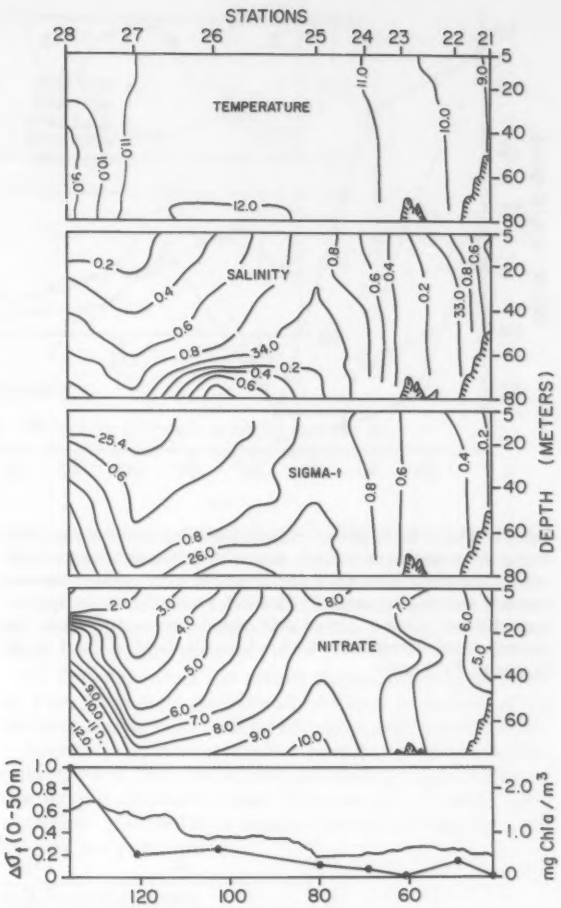

FIG. 6. Vertical profiles of temperature, salinity, sigma-*t*, nitrate, continuous in vivo surface chlorophyll (●—●), and the difference in density between the surface and 50 m (—) for stations 21–28, November 1979.

from selected inshore stations (Fig. 8). Each cruise separated naturally into two groupings. The inshore stations (4–7) on the first transect of both cruises fell at the cooler, less saline end, but not without some overlap. The most important difference distinguishing the two cruises is the much wider vertical range in both variables for November. That range resulted in a greater spread in density, which in turn contributed to reduced mixing.

Finally, summer–fall chlorophyll distributions are compared in Fig. 9, where continuous surface traces from the same transect are presented for July and November. The curves are clearly out of phase. The summer peak was well defined, with concentrations in excess of 12 mg/m^3. With the exception of one point, density differences between the surface and 50 m gradually increased from essentially zero to almost 2.5 offshore. No relationship is obvious between the two variables, although Fournier et al. (1984) have shown that the gradual increase in stratification, which marks the frontal zone, is the contributing factor. In November, both chlorophyll and density are much lower but the influence of localized stratification is more clearly delineated.

Discussion

In late fall, the waters overlying temperate continental shelves are usually well mixed, contain abundant nutrients, and receive increasingly less sunlight. The combined effect of a deep mixed layer and reduced sunlight is to produce relatively low homogeneous concentrations of chlorophyll. This condition is depicted in the December 1978 observations, presented earlier. However, any influence that causes increased stratification during this period will permit phytoplankton to better utilize available sunlight and nutrients, and to exceed background chlorophyll levels by growing more rapidly than less well stabilized regions (Fournier et al. 1979). That is the situation observed in November 1979.

In November, chlorophyll was higher at the offshore end of each transect. The slight increase in stratification that made that possible was due to the intrusion of warm saline water that originated from the slope region (Fournier et al. 1977; Houghton et al. 1978) or the Gulf of Maine (Hopkins and Garfield 1979). The westward flowing longshore current would have had

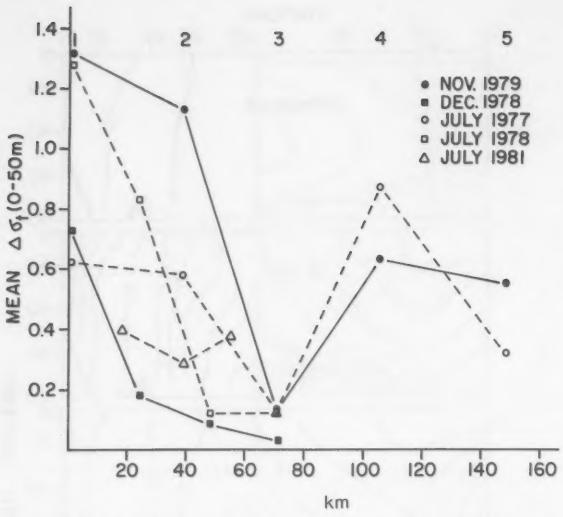

FIG. 7. Plot of the difference in density between the surface and 50 m averaged for the innermost three stations on all transects from two fall cruises and three summer cruises (Fournier et al. 1984). Since all transects are not geographically identical, the abscissa is the approximate distance along a curved path going from east to west. The numbers at top correspond to the five transects shown in Fig. 1 for the November 1979 cruise.

little effect on the outer stations, since it was contained principally within the 110-m isobath (Smith 1983). This is thought to be a temporary condition, since with the approach of cooler weather, convective overturn would increase, the mixed layer would deepen, and the mild stratification visible in November would gradually merge into the well-mixed condition of December. Once deep mixing occurred that late in the year, no replacement in buoyancy would be expected until warming in spring, or from an episodic event such as the encroachment of a gulf stream eddy (Smith 1978). Except for the possibility of isolated events, offshore stations would gradually become indistinguishable from much of the shelf at that time of the year.

The inshore is different because it is strongly influenced by the continuing inflow from the Nova Scotia current. Chlorophyll concentrations are in some places 5 times higher in November than December because the mixed layer was only 40% as deep. Reduction of the mixed layer resulted from an influx of relatively fresh water into the area where it rested over the existing denser water. The current contributed to a buoyancy flux. Smith (1983) has shown that the role of temperature is secondary to that of salinity in controlling local mixing and density distribution. This conclusion was based on current meter data gathered from a line of four sites across the western end of the shelf (roughly equivalent to our stations 14–20), plus two more sites upstream of Roseway (Fig. 1). This array was in position at the time our November observations were made. The longshore current, denoted by clear signals

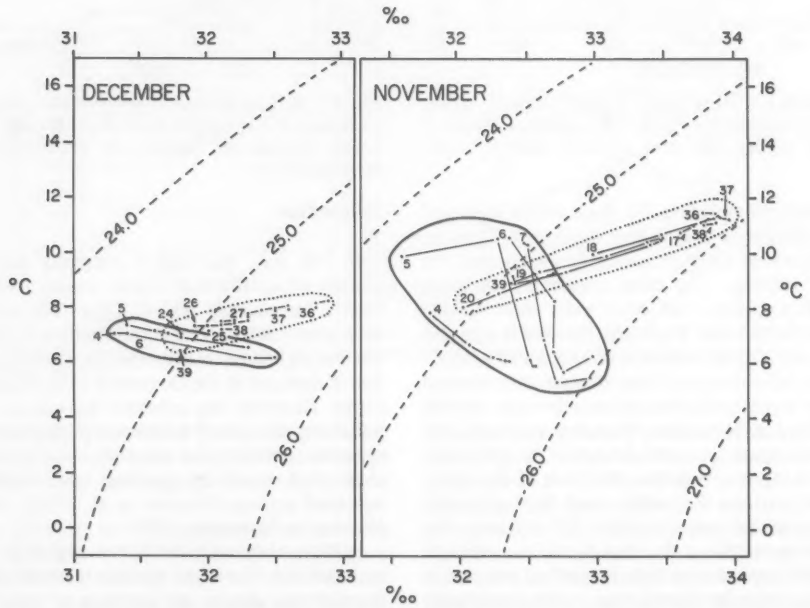

FIG. 8. Temperature–salinity diagram showing stations 4–6, 24–27, and 36–39 for December 1978 and stations 4–7, 17–20, and 36–39 for November 1979. Each station was ideally represented by five points between 10 and 50 m, although vertical homogeneity reduced that representation to one point in several cases. The station number identifies the 10-m point.

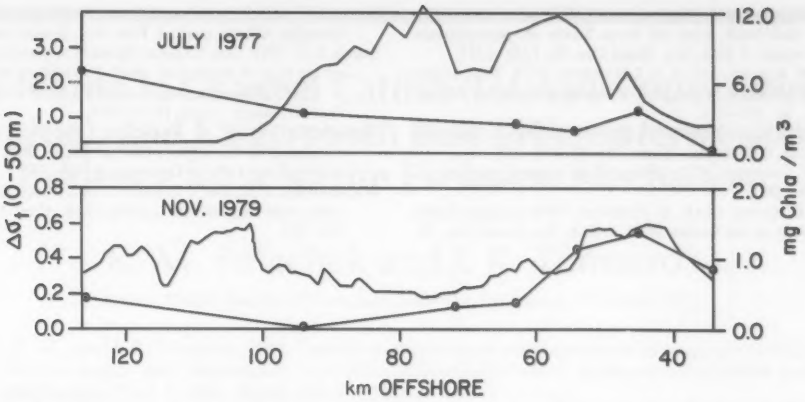

FIG. 9. Continuous in vivo surface chlorophyll (●—●) and the difference in density between the surface and 50 m (—) for the same transect (stations 14–20, November, Fig. 1). Note differences in density and chlorophyll scales.

in temperature ($-\Delta 3°C$), salinity ($-\Delta 1.5‰$), and density ($-\Delta 1.0\sigma_t$), arrived off Cape Sable on 30 October, approximately 1 wk prior to our measurements. Two weeks later (November 14), a second pulse was observed in which the salinity and density dropped a further 1.5‰ and $1.0\sigma_t$, while temperature remained unchanged. Between 6 and 19 December, an intense meteorological low accompanied by reversal in wind direction reduced the westward flow of the longshore current and reintroduced temperature and salinity conditions identical to those prior to 30 October. After 19 December, the westward flow resumed and remained uninterrupted, except for a few minor reversals, until mid-February.

We suggest that higher inshore chlorophyll concentrations in November result from the introduction of stratification via the mechanism of a buoyancy flux. The influx and overlay of lighter water on the denser water already there created a very sharp pycnocline at an unseasonably shallow depth. This applies only to the first two sections (stations 4–20), since the intense tidal mixing encountered farther westward (Fig.7) is sufficient to mix the water column despite the continuous inflow of low-salinity water. An analogous situation has been described by Dooley (1981) for the northwestern North Sea. There, the inflowing Fair Isle current enters the North Sea between Orkney and Shetland and contributes to the hydrographic and biological character of that area. The incoming water influences the density distribution, counteracts intense tidal mixing in summer, while at the same time replenishing nutrients for the phytoplankton. Dooley estimated that during a 100-d summer, production was augmented to the equivalent of the full spring flowering. Off Nova Scotia, the general result of this buoyancy flux is similar, i.e. to lengthen the productive period and forestall the arrival of deep mixing in late fall with its attendant low concentrations of chlorophyll.

The December 1978 observations did not show any enhancement in chlorophyll for the following reasons, which are not necessarily mutually exclusive:

(1) The longshore current arrived after our cruise in 1978. According to P. C. Smith (Bedford Institute, pers. comm.), historical records indicate that the onset can vary between October and January.

(2) During our cruise, a current reversal could have been underway. Evidence for such an occurrence is present in the 1979 current meter record (Smith 1983). This might explain why temperature and salinity are similar both years, but water column distribution and stratification are so different.

(3) A westward flow could have been underway but convection resulting from near-winter conditions could have worked to offset the buoyancy input.

(4) The temperature and salinity characteristics of the water off Cape Sable were insufficiently different from those of the incoming current to promote the necessary shallow mixed layer.

A number of questions remain to be answered about this area, especially with regard to within- and between-year consistency. One thing is abundantly clear: this is an area of considerable variability, governed by a complex mixture of both high- and low-frequency variables.

Acknowledgements

We are deeply indebted to a large number of students from the Department of Oceanography, Dalhousie University, too numerous to name, who voluntarily contributed a great deal of time and effort to the success of this program. In addition, we very much appreciate the technical assistance provided by the Coastal Oceanography Group of the Bedford Institute of Oceanography. Finally, thanks are due to the Captain, Officers, and Crew of the C.S.S. *Dawson*. This work was supported by grants from the Natural Sciences and Engineering Research Council of Canada plus subventions from the Department of Fisheries and Oceans.

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Toxicity of Nitrite to Channel Catfish (*Ictalurus punctatus*), Tilapia (*Tilapia aurea*), and Largemouth Bass (*Micropterus salmoides*): Evidence for a Nitrite Exclusion Mechanism

R. M. Palachek and J. R. Tomasso

Aquatic Station, Southwest Texas State University, San Marcos, TX 78666, USA

Palachek, R. M., and J. R. Tomasso. 1984. Toxicity of nitrite to channel catfish (*Ictalurus punctatus*), tilapia (*Tilapia aurea*), and largemouth bass (*Micropterus salmoides*): evidence for a nitrite exclusion mechanism. Can. J. Fish. Aquat. Sci. 41: 1739–1744.

The 96-h median lethal concentrations of nitrite to channel catfish (*Ictalurus punctatus*), tilapia (*Tilapia aurea*), and largemouth bass (*Micropterus salmoides*) under similar water quality conditions were 7.1 ± 1.9, 16.2 ± 2.3, and 140.2 ± 8.1 mg NO_2-N/L (mean ± SE), respectively (pH 7.7–8.2; temperature 23°C). During 24-h sublethal exposures to nitrite, methemoglobin concentrations in the blood of all three species generally increased with increasing nitrite concentrations. Channel catfish and tilapia concentrated nitrite in their blood above environmental levels and generated higher methemoglobin concentrations than largemouth bass at all nitrite concentrations tested. Largemouth bass did not develop elevated methemoglobin concentrations until NO_2-N concentrations reached 48.7 mg/L, and plasma nitrite concentrations in largemouth bass were never observed higher than environmental concentrations. These data indicate that differences in resistance to nitrite among species may be partially due to a differential ability of some species to prevent the concentration of nitrite in the plasma.

Dans un test de 96 h, la concentration létale médiane de nitrite pour la barbue de rivière (*Ictalurus punctatus*), le télapie (*Tilapia aurea*) et l'achigan à grande bouche (*Micropterus salmoides*) gardés dans le même type d'eau était de 7,1 ± 1,9, 16,2 ± 2,3 et 140,2 ± 8,1 mg NO_2-N/L (moyenne ± er.-t.), respectivement (pH entre 7,7 et 8,2 ; température : 23°C). Durant un test de 24 h au cours duquel on a administré une dose de nitrite sublétale, la concentration de méthémoglobine sanguine a en général augmenté chez les trois espèces en fonction de l'élévation de la dose de nitrite. Chez la barbue de rivière et le tilapie, la concentration de nitrite dans le sang dépassait celle du milieu et la teneur en méthemoglobine a atteint une valeur plus élevée que chez l'achigan à grande bouche pour toutes les doses de nitrite testées. Chez l'achigan à grande bouche, la concentration de méthémoglobine ne s'est élevée qu'à la dose de 48,7 mg NO_2-N/L et le nitrite plasmatique n'a jamais dépassé la contration dans le milieu. Ces données indiquent que les différences de résistance au nitrite observées entre diverses espèces pourraient être dues en partie à la capacité d'empêcher ce composé d'atteindre le sang.

Received March 26, 1984
Accepted August 17, 1984
(J7734)

Reçu le 26 mars 1984
Accepté le 17 août 1984

Low concentrations of environmental nitrite are toxic to many species of fishes (Russo and Thurston 1977). Nitrite may reach toxic concentrations in recirculating aquaculture systems where ammonia, the major nitrogenous waste product of fishes, is concentrated, converted first to nitrite, and then to less toxic nitrate. Concentrations of nitrite can also increase to toxic levels in streams receiving effluent from wastewater treatment plants due to an imbalance in the nitrification process.

Nitrite enters the fish through the gills and passes into the circulatory system (Perrone and Meade 1977). The best known effect of nitrite is the conversion of hemoglobin to methemoglobin, a derivative incapable of binding and transporting oxygen (Brown and McLeay 1975; Wedemeyer and Yasutake 1978). In effect, fish with elevated levels of methemoglobin may suffer from anoxia (Russo et al. 1974; Huey et al. 1980; Tomasso et al. 1981).

The literature suggests that the toxicity of nitrite varies greatly among fish species. For example, 96-h median lethal concentrations (LC50) range from 0.2 mg nitrite-nitrogen (NO_2-N)/L for rainbow trout (*Salmo gairdneri*) (Russo and Thurston 1977) to 86 mg NO_2-N/L (calculated from NO_2^- data reported by author) for bluegill (*Lepomis macrochirus*) (Huey et al. 1982). There also appear to be toxicity variations within species. The reported 24-h LC50 values for channel catfish (*Ictalurus punctatus*) include 1.5 mg NO_2-N/L (calculated from NO_2^- data) (Tomasso et al. 1980), 10.3 mg NO_2-N/L (calculated from NO_2^- data) (Konikoff 1975), and 26.2 mg NO_2-N/L (calculated from NO_2^- data) (Colt and Tchobanoglous 1976). These differences are probably attributable to the different water quality characteristics that exist at the individual research facilities and to genetically based differences in nitrite susceptibility among species. Toxicity depends on environmental pH, alkalinity, calcium, and chloride concentrations (Perrone and

TABLE 1. Water quality characteristics in test aquaria during nitrite toxicity tests (range, mean, or mean ± SE). Number of tanks sampled is given in parentheses.

Character	24 h	48 h	72 h	96 h
pH[a]	7.7–8.1 (88)	7.7–8.1 (32)	7.7–8.1 (25)	7.7–8.2 (20)
DO (mg/L)[b]	7.9±0.1 (61)	8.1±0.1 (36)	8.2±0.0 (24)	8.1±0.0 (25)
Temperature (°C)[b]	23 (42)	23 (20)	23 (20)	23 (20)
Alkalinity as $CaCO_3$ (mg/L)[c]	222.7±5.0 (24)	203.6±4.5 (29)	181.2±5.9 (20)	165.6±3.9 (27)
Hardness as $CaCO_3$ (mg/L)[c]	254.8±3.5 (37)	234.5±4.4 (19)	217.7±4.6 (21)	202.4±3.6 (27)
Nitrite (% nominal)[d]	101.6±1.0 (79)	99.7±1.1 (40)	102.0±2.3 (22)	101.6±1.2 (20)

[a]pH meter.
[b]Dissolved oxygen/temperature meter.
[c]Hach Chemical Company (1973).
[d]Azo-dye method (USEPA 1974).

Meade 1977; Russo and Thurston 1977; Tomasso et al. 1980; Russo et al. 1981; Huey et al. 1982).

Limited information is available on comparisons of different species of fishes under similar water quality conditions which would allow partitioning environmental from species differences in resistance to the toxin. The purpose of this study was to determine the effects of nitrite on three species of freshwater fishes under similar water quality conditions. Specific objectives were to determine (1) the LC50 for three species of fishes selected to represent three different families, Ictaluridae (channel catfish), Centrarchidae (largemouth bass, *Micropterus salmoides*), and Cichlidae (tilapia, *Tilapia aurea*), (2) methemoglobin levels in the three species after exposure to various environmental nitrite concentrations, and (3) plasma nitrite concentrations in fish after exposure to various environmental concentrations.

Materials and Methods

Largemouth bass were obtained from the National Fish Hatchery and Technology Center, San Marcos, Texas. Channel catfish were acquired from the Texas Parks and Wildlife Department, San Marcos Fish Hatchery, and tilapia from the Texas A & M University Aquaculture Research Center, College Station, Texas. All fish were acclimatized for at least 4 wk prior to testing in 252-L fiberglass tanks supplied by well water (temperature 23°C; pH 7.2; hardness 310 mg/L as $CaCO_3$; dissolved oxygen > 6.0 mg/L; chloride 22 mg/L; NO_2-N < 0.01 mg/L) at a flow rate of seven turnovers per hour. Fish were fed a commercial fish food (40% protein) ad libitum every 48 h. Feeding was discontinued 24 h prior to transferring fish into experimental aquaria.

All tests were conducted in 30-L glass aquaria placed in a 23°C water bath. Test water came from the same source as holding water and was constantly aerated to maintain dissolved oxygen levels near saturation. Fish were placed in experimental aquaria and acclimatized for 24 h prior to adding reagent grade sodium nitrite. Water characteristics for LC50's were measured in randomly selected aquaria every 24 h throughout the tests. Water quality for methemoglobin and plasma nitrite determinations was measured at 0 and 24 h in all aquaria (Table 1).

Twenty-four-, 48-, 72-, and 96-h LC50 concentrations were determined for channel catfish and largemouth bass using 10 fish per aquarium; 5 fish were used in the tests on tilapia. Nitrite concentrations were increased from aquarium to aquarium by a geometric progression factor of 1.6 in a series of five aquaria per species (from 2.7 to 28.7 mg NO_2-N/L for channel catfish, 11.9 to 77.9 mg NO_2-N/L for tilapia, and 57.1 to 374.2 mg NO_2-N/L for largemouth bass) for LC50 determinations. A sixth aquarium in each series served as a nitrite-free control. Dead fish were removed every 24 h and weighed to the nearest 0.1 g. Because nitrite tolerance may vary with size (Russo et al. 1974; Smith and Williams 1974; Perrone and Meade 1977; Palachek and Tomasso 1984), at least in the younger stages, testing was conducted using individuals of approximately the same weight (channel catfish 3.0 ± 0.1 g; tilapia 3.4 ± 0.2 g; largemouth bass 2.8 ± 0.0 g (mean ± SE)). Median lethal concentrations were estimated using the method of Thompson (1947). Each LC50 series was repeated three or more times for each species.

Methemoglobin and plasma nitrite concentrations were determined using five fish per aquarium exposed to nitrite concentrations ranging from 1.5 to 194.9 mg/L (geometric progression factor = 2). After 24 h of exposure, fish were weighed, the caudal peduncle was severed, and blood was collected into capillary tubes from the haemal arch. Methemoglobin concentrations were determined spectrophotometrically (Evelyn and Malloy 1938) after blood samples were lysed, and centrifuged to remove turbidity. Total hemoglobin was determined according to Hainline (1958). In the determination of methemoglobin, at least 10 channel catfish or largemouth bass from each concentration of nitrite were sampled with the exception of the 24.4 mg NO_2-N/L concentration for channel catfish where 5 fish were used. Five or more tilapia were used from each nitrite concentration for analysis. Average fish weights used in methemoglobin analysis were 12.6 ± 0.3 g for channel catfish, 31.2 ± 2.2 g for tilapia, and 19.6 ± 1.0 g for largemouth bass.

Plasma nitrite levels were determined by a modification of the azo-dye method for water analysis (USEPA 1974). Fish blood was removed as before into heparinized capillary tubes, which were centrifuged and broken at the plasma–cell interface. Plasma (20 µL) was transferred to spectrophotometer tubes containing 3 mL of deionized water and 0.2 mL of azo-dye

reagent. After 10 min, absorbance at 540 nm was determined. As an internal assay control, 20 μL of fish plasma with a known amount of nitrite added to it, was similarly assayed. In addition, randomly selected assays were spiked with known amounts of nitrite at low, intermediate, and high levels after the initial determination of plasma nitrite. In all cases, nitrite concentrations determined were 95–106% of the expected value. The number of fish sampled for plasma nitrite analysis varied from 8 to 13 channel catfish or largemouth bass and at least 5 tilapia for each environmental nitrite concentration. Average weights of fish used in plasma nitrite analysis were as follows: channel catfish, 10.6 ± 0.2 g; tilapia, 21.7 ± 1.0 g; largemouth bass, 19.1 ± 0.5 g.

Analysis of variance followed by a Student–Newman–Keuls multiple-range test (Woolf 1968) was employed to test for differences among species. An $\alpha = 0.05$ was established as the level for significance in all tests.

Results and Discussion

Median lethal concentrations, summarized in Fig. 1, were significantly different among all three species tested under similar water quality conditions after 96 h of exposure. Channel catfish were the least resistant to nitrite of the species tested with a 96-h LC50 value of 7.1 ± 1.9 mg NO_2-N/L. Tilapia showed an intermediate tolerance for nitrite compared with the other two species with a 96-h LC50 of 16.2 ± 2.3 mg NO_2-N/L. Largemouth bass had a 96-h LC50 of 140.2 ± 8.1 mg NO_2-N/L. In a previous study under the same experimental conditions, fathead minnows (*Pimephales promelas*) weighing 3.1 g had a 96-h LC50 of 43.1 ± 2.7 mg NO_2-N/L (Palachek and Tomasso 1984). The values reported here for largemouth bass are higher than those reported for any other freshwater fish species (see review by Russo and Thurston 1977).

The 24-h dose–response studies showed that methemoglobin levels increased as environmental nitrite levels increased, with the exception of the largemouth bass whose methemoglobin levels did not increase until nitrite concentrations reached 48.7 mg/L (Fig. 2). The channel catfish were most susceptible and had the highest methemoglobin levels compared with the other species. Channel catfish exposed to 12.2 and 24.4 mg NO_2-N/L had methemoglobin levels of 84.5 ± 4.6 and 95.3 ± 2.5% of total hemoglobin, respectively.

Several channel catfish at 12.2 and 24.4 mg NO_2-N/L remained motionless on the bottom of the aquaria and had methemoglobin levels of 100%. Perrone and Meade (1977) have suggested that it is possible for fish in "good" physical condition with high stores of glycogen to obtain the majority of their required energy from anaerobic glycolysis. Also, fish can decrease oxygen requirements by reduced activity and could meet the lowered demand through oxygen dissolved in the plasma, allowing them to tolerate high methemoglobin levels for long periods of time (Fox 1954). Methemoglobin levels in tilapia (69.5 ± 6.5% after 24 h of exposure to 12.2 mg NO_2-N/L) also increased with increasing nitrite concentrations and were consistently intermediate to the channel catfish and largemouth bass levels.

Largemouth bass exposed to 97.4 and 194.9 mg NO_2-N/L showed levels of only 38.4 ± 4.4 and 47.6 ± 3.2% methemoglobin, respectively. Two difficulties were experienced in obtaining methemoglobin values for largemouth bass. First, some blood samples became turbid after the addition of neutral sodium cyanide reagent and remained so after centrifugation.

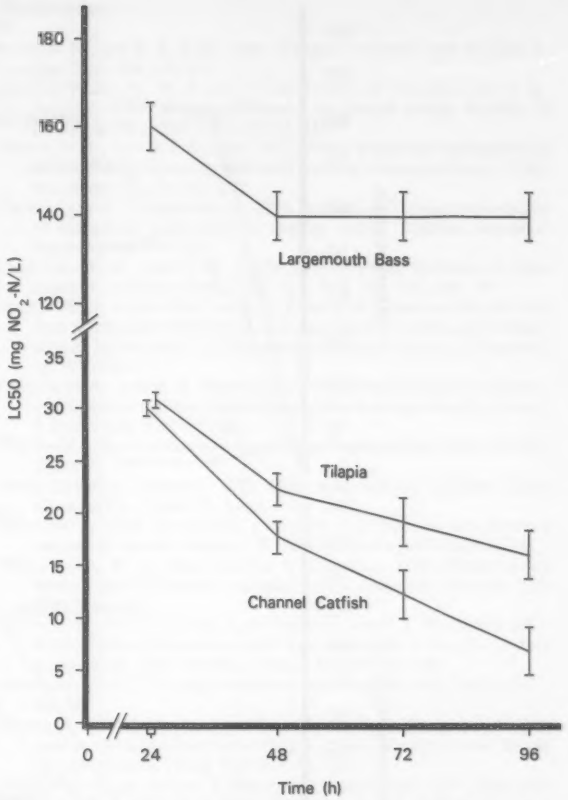

FIG. 1. Median lethal concentrations (LC50) of nitrite for three fish species (mean ± SE). Twenty-four-, 48-, and 72-h LC50's for channel catfish and tilapia were statistically similar, and both statistically different from largemouth bass. All three species LC50's were statistically different from each other at 96 h.

Second, largemouth bass were difficult to bleed because of a tendency for the blood to clot at a much faster rate than the blood of the other two species. Furthermore, blood appeared to clot even more quickly at the higher levels of nitrite exposure. Therefore, largemouth bass with lower methemoglobin levels may have been preferentially sampled, and our reported methemoglobin values for largemouth bass exposed to the higher nitrite concentrations may be artificially low.

The ability of largemouth bass to survive and to maintain low blood methemoglobin levels during exposure to extremely high levels of nitrite was unexpected, particularly since several reports indicate that fish actively concentrate nitrite in their blood (Bath and Eddy 1980; Meade and Perrone 1980). Rainbow trout may concentrate nitrite as much as 60 times more than environmental concentrations (Margiocco et al. 1983). Our results indicate that channel catfish and tilapia concentrate nitrite in the plasma (Fig. 2) as do rainbow trout. Channel catfish and tilapia exposed to 24.4 mg NO_2-N/L for 24 h had levels of 76.9 ± 5.0 and 61.3 ± 7.9 mg plasma nitrite/L, respectively. Tilapia consistently concentrated nitrite to a lesser extent than did the channel catfish. Plasma nitrite levels in largemouth bass did not differ from control levels until environmental concentrations reached 48.7 mg NO_2-N/L or greater. Largemouth bass exposed to 97.4 and 194.9 mg

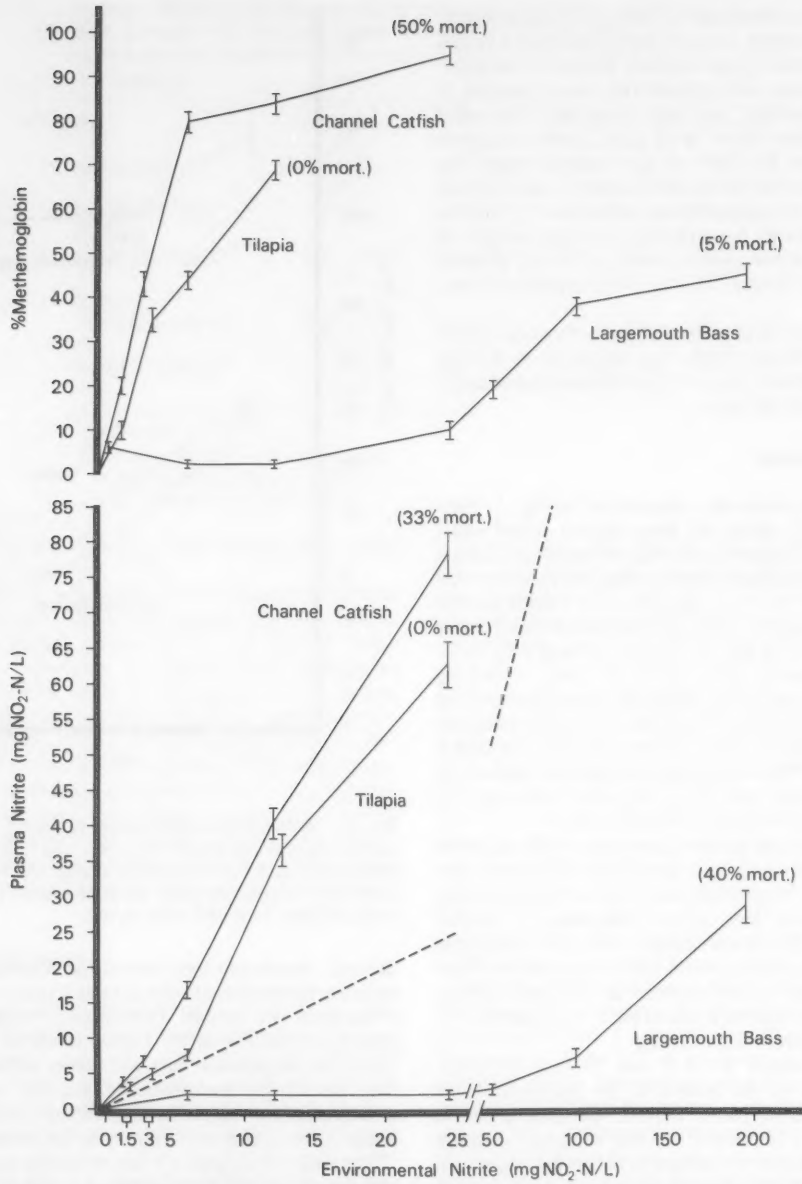

FIG. 2. Methemoglobin as percent of total hemoglobin and plasma nitrite concentrations in three species of fishes exposed to various concentrations of environmental nitrite (mean ± SE). The broken line represents equal environmental and plasma nitrite concentrations. Methemoglobin percentages for all three species were statistically different at all concentrations tested with the exception of 3.0 mg NO_2-N/L where channel catfish and tilapia were similar. Plasma nitrite concentrations for channel catfish and tilapia were similar at 1.5, 3.0, and 12.2 mg environmental NO_2-N/L. Channel catfish and tilapia were statistically different from largemouth bass at 12.2 mg/L and all species were statistically different at 6.1 and 24.4 mg/L.

NO_2-N/L had measured levels of only 6.8 ± 2.0 and 27.7 ± 3.5 mg plasma nitrite/L, respectively. Plasma nitrite levels in largemouth bass were significantly lower than those of the other two species at all environmental concentrations. Furthermore, the largemouth bass never had plasma nitrite concentrations higher than environmental levels as did the other species.

These data indicate that there is a mechanism in largemouth bass that excludes nitrite from the plasma. To our knowledge this is the first report of a nitrite exclusion mechanism in fish. Previous reports suggest that environmental nitrite is actively pumped into freshwater fish by the active transport mechanism which ordinarily transports chloride ions (Perrone and Meade

1977; Tomasso et al. 1979; Bath and Eddy 1980; Meade and Perrone 1980). A relationship between plasma nitrite concentrations and the number of lamellar chloride cells has been established in rainbow trout (Krous et al. 1982). Variations among species in the numbers and differential selectivity of chloride cells to nitrite could account for a portion of the differences in nitrite toxicity among species. In Fig. 2, it is apparent that methemoglobin and plasma nitrite levels follow similar curves for each species and appear to be correlated, as has been reported in nitrite-exposed rainbow trout (Eddy et al. 1983).

The finding that largemouth bass exclude nitrite from their plasma raises a question concerning the primary toxic mechanism of nitrite. Low plasma nitrite concentrations and the corresponding low methemoglobin levels in largemouth bass at high (97.4, 194.9 mg/L) environmental nitrite exposures support the suggestion, as made by other investigators (Smith and Williams 1974; Brown and McLeay 1975; Crawford and Allen 1977), that some toxic mechanism other than methemoglobinemia is associated with death. Methemoglobinemia may be a major mechanism in fish that concentrate nitrite in their plasma such as channel catfish and tilapia, but largemouth bass may succumb to another toxic mechanism. One mechanism that may affect a species at extreme environmental concentrations (194.9 mg/L) could be gill damage. Gill hypertrophy, hyperplasia, and lamellar separation were noted in steelhead trout (*Salmo gairdneri*) after a 3-wk exposure to 0.06 mg NO_2-N/L (Wedemeyer and Yasutake 1978). A second mechanism that may affect a species is the concentration of nitrite in organs as suggested by Margiocco et al. (1983).

Another possibility that must be considered is species differences in the tolerance to different methemoglobin levels (Russo 1980). It seems more likely that different methemoglobin levels may cause mortality depending on species differences in oxygen demand that results from metabolic activity, dominant behavior (Perrone and Meade 1977), and sensitivity to environmental oxygen concentrations (Bowser et al. 1983; Tomasso et al. 1981).

Our results confirm that toxicity of nitrite varies considerably among species tested under similar water quality conditions as suggested by McCoy (1972) and Russo and Thurston (1977). The data also indicate that these differences are related to the extent to which nitrite is concentrated in the plasma, and the associated blood methemoglobin levels. Therefore, channel catfish have a lower resistance to nitrite than tilapia or largemouth bass because nitrite is more concentrated in catfish plasma. Among the three species, largemouth bass has the greatest resistance to environmental nitrite as well as the lowest methemoglobin levels due to lower plasma nitrite concentrations. The low plasma nitrite levels may be indicative of a more selective chloride uptake cell located in the gills, resulting in exclusion of nitrite.

Acknowledgements

Fish were provided by Texas Parks and Wildlife Department (San Marcos Fish Hatchery), Texas A & M University Aquaculture Research Center, College Station, Texas, and the National Fish Hatchery and Technology Center (NFHTC), San Marcos, Texas. NFHTC also provided wet laboratory facilities for this study. Financial support was provided by a Southwest Texas State University Faculty Research grant to J. R. Tomasso. J. R. Koke, R. A. Short, and G. J. Carmichael critically reviewed this manuscript.

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Intraspecific Resource Partitioning by Yellow Perch (*Perca flavescens*) in a Stratified Lake[1]

Mark B. Sandheinrich and Wayne A. Hubert[2]

Iowa Cooperative Fishery Research Unit,[3] Iowa State University, Ames, IA 50011, USA

Sandheinrich, M. B., and W. A. Hubert. 1984. Intraspecific resource partitioning by yellow perch (*Perca flavescens*) in a stratified lake. Can. J. Fish. Aquat. Sci. 41: 1745–1752.

Summer habitat use and relative abundances of different size classes of yellow perch (*Perca flavescens*) were determined using gill nets set in the main basin, deep bays, and shallow bays of a lake. Niche overlap indices were used to quantify resource use patterns. Size classes spatially segregated into different habitats, but not different depths within a habitat type. Segregation of sexes at different depths was observed with females occupying warm, shallow areas, whereas males were more common in cool, deep water. Formation of an anoxic hypolimnion restricted perch to the epilimnion in late summer, but patterns of habitat segregation observed prior to thermocline formation were maintained. Food partitioning was relatively unimportant in reducing niche overlap. Spatial segregation of perch size classes and sexes may compensate for high diet overlap between conspecifics and reinforces the importance of habitat partitioning in structuring fish communities.

On a étudié l'utilisation de l'habitat estival et l'abondance relative des différentes catégories de taille de la perchaude (*Perca flavescens*) par des échantillonnages au filet maillant effectués dans le bassin principal, les baies profondes et les baies peu profondes d'un lac. Pour quantifier l'utilisation des ressources, on s'est servi d'indices de recoupement des niches. Les différentes catégories de taille occupaient des habitats distincts, mais non diverses profondeurs dans un même type d'habitat. Les sexes occupaient des profondeurs différentes : en effet, les femelles se trouvaient dans les eaux chaudes, peu profondes, tandis que les mâles étaient plus communs en eau froide et profonde. En raison de la formation d'un épilimnion pauvre en oxygène, les perchaudes étaient confinées à l'hypolimnion vers la fin de l'été, mais la répartition suivant l'habitat est demeurée la même qu'avant l'apparition de la thermocline. Le partage de la nourriture ne réduisait le recoupement des niches que dans une mesure relativement négligeable. Le fait que les poissons de sexe et de catégorie d'âge différents soient séparés pourrait compenser l'important recoupement des ressources nutritives des perchaudes ; cet arrangement confirme l'importance de la séparation des habitats dans les communautés de poissons structurées.

Received October 19, 1983
Accepted August 20, 1984
(J7577)

Reçu le 19 octobre 1983
Accepté le 20 août 1984

Ecological segregation of species, and size classes within a single species, by differences in resource utilization is common in freshwater fish communities. Previous studies of resource partitioning in lentic systems have concentrated on fish inhabiting either the littoral or limnetic zone (e.g. Werner et al. 1977, 1978; Brandt et al. 1980; Crowder et al. 1981). But few studies have considered resource partitioning by a species simultaneously occupying both of these areas. Studies of intraspecific resource partitioning can offer insight into the dimensions of an organism's niche and are prerequisite to understanding complex interspecific patterns of resource use within a fish community.

Competition may be an important factor influencing percid community structure (Forney 1977; MacLean and Magnuson 1977). Stunted growth is common in perch populations and is often attributed to intraspecific competition. Previous studies of resource partitioning by perch have dealt with slow-growing populations in shallow, eutrophic lakes (Keast 1977a; Persson 1983). In this study we examine patterns of resource use by different sexes and size classes of yellow perch (*Perca flavescens*) inhabiting the littoral and limnetic zones of a stratified glacial lake. Specifically, we addressed the relative importance of food and habitat partitioning in reducing niche overlap, and assessed the effects of thermocline formation on resource use.

The yellow perch is a demersal species inhabiting both littoral and limnetic zones of North American temperate lakes. Perch are gregarious, forming schools segregated by size (Hasler and Bardach 1949) and often by sex (Jobes 1952; Wells and Jorgenson 1983). They are most abundant in lakes with moderately dense macrophytes, but are not closely associated with specific habitat types (Engel and Magnuson 1976). Yellow perch are opportunistic predators on a wide array of food organisms. Diet can vary with age (Keast 1977a), time of year, and location within a lake (Hubert and Sandheinrich 1983).

[1]Journal paper No. J-11086 of the Iowa Agriculture and Home Economics Experiment Station, Ames, IA. Project No. 2345. Financed by the Iowa State Conservation Commission.

[2]Present address: Wyoming Cooperative Fishery and Wildlife Research Unit, University of Wyoming, Laramie, WY 82071, USA.

[3]Jointly supported by Iowa State University, the Iowa State Conservation Commission, and the U.S. Fish and Wildlife Service.

Methods

Lake West Okoboji is a eutrophic, dimictic, glacial lake in northwestern Iowa (43°23′N, 95°11′W). The 1540-ha lake has mean and maximum depths of 11.9 and 42.7 m (Bachmann et al. 1966). Submersed aquatic macrophytes extend downward to a depth of 6.5 m (Crum and Bachmann 1973). Thermal stratification occurs in early summer, and oxygen concentrations decline in the hypolimnion after thermocline formation. The lake's large bays, deep V-shaped central trough, and irregular shoreline make it unusual among midwestern prairie lakes and provide an opportunity to study resource use by fish in a structurally complex environment. Birge and Juday (1922), Stromsten (1928), and Bachmann and Jones (1974) described the lake's limnological and morphological characteristics.

Percids, centrarchids, and esocids dominate the diverse fish community; the yellow perch predominates in the creel. Temperature and oxygen concentrations seem to govern the summer distribution of yellow perch within the lake, and restrict them to cool, oxygenated depths above the thermocline (Hubert and Sandheinrich 1983).

Five locations, representing three habitat types, were sampled: shallow bays (Little Millers Bay and Little Emerson Bay), deep bays (Millers Bay and Emerson Bay), and the main basin. Sampling was conducted from June 8 to July 6 (early summer) and July 28 to August 18, 1981 (late summer). These sampling periods were chosen to assess yellow perch distributions before and after the development of an anoxic hypolimnion in mid-July. Yellow perch were sampled with four monofilament gill nets (10 m long × 1.8 m deep), each with a single mesh size 1.9, 2.5, 3.2, or 3.8 cm (bar-measure). Nets of the four mesh sizes were set simultaneously on the bottom and parallel to shore. Nets were set on the lake bottom at depth contours of 2.5, 5, 10, and 15 m in the main basin, 2.5, 5, and 9 m in the deep bays, and 2.5 m in the shallow bays. One depth within one location was sampled in an evening. The order in which the locations and depth contours were sampled was randomly determined. Nets were set 1.5 h before sunset and lifted 2 h later to coincide with the twilight feeding period of the perch. Samples in Emerson Bay and Little Emerson Bay were collected about 1 wk after those of the other three locations.

Water temperature and dissolved oxygen concentrations (modified Winkler technique) were measured during the 2-h interval at the depth sampled at each netting location. Temperature and oxygen profiles were also obtained biweekly from the main basin with a resistance thermometer and a dissolved oxygen meter. A Peterson dredge was used to sample the substrate at each netting location, once during early and late summer, to qualitatively classify the bottom type as predominantly silt, sand, gravel, or cobble. Identification of substrate type and a visual estimate of submersed macrophyte density were made from the boat during sampling and with SCUBA in late July.

The number of yellow perch captured per hour per 10-m net was the catch per unit effort (CPUE) used to estimate relative abundance. Captured perch were measured to the nearest 1.0 mm (total length), sexed by gonadal inspection, and grouped by collection site and 25-mm total length intervals. Stomachs were excised and preserved in 10% formalin. Food organisms were separated later into taxonomic groups, dried at 65°C for 24–48 h, and weighed to the nearest 0.1 mg.

Measures of niche overlap were used to quantify resource use by the various perch size classes and to facilitate comparisons of resource use between sampling periods and habitats. Overlap indices assess the degree to which two organisms share a common resource but do not directly measure competition.

The diets of different size classes of yellow perch, within specific depths and habitats, were compared by computing the percentage of overlap (α) according to Schoener (1970):

$$\alpha = 100[1 - 0.5 \Sigma |P_{x,i} - P_{y,i}|]$$

where $P_{x,i}$ is the proportion of the ith prey in the diet of size class x and $P_{y,i}$ is the proportion of the ith prey in the diet of size class y.

Overlap in habitat use by size classes, at different depths within a habitat (α_W), was measured for perch in the main basin and deep bays during each period:

$$\alpha_W = 100[1 - 0.5 \Sigma |P_{x,i} - P_{y,i}|]$$

where $P_{x,i}$ is the proportion of size class x at the ith depth and $P_{y,i}$ is the proportion of size class y at the ith depth within a habitat. Between-habitat overlap (α_B) of size classes was calculated in a manner similar to α_W, but with the proportion of any size class (P_x, P_y) at the ith depth being a proportion of the combined total numbers of fish of that size class in the main basin, Millers Bay, and Little Millers Bay, or Emerson Bay and Little Emerson Bay. If yellow perch size classes are randomly distributed among habitats and among depths within habitats, we would expect α_W to be equal to α_B. An α_B value significantly less than a corresponding α_W would indicate that size classes reduce spatial overlap by the occupation of different habitats. Conversely, if $\alpha_W < \alpha_B$, then size classes occupy similar habitats but reduce spatial overlap by occupying different depths within a habitat.

Schoener's equation (1970), in its present form, does not account for the sexual component of interclass overlap, which is an integral part of α_W. Therefore, the equation was modified to calculate the percentage overlap between males and females of different size classes within a habitat, α_{WS}:

$$\alpha_{WS} = 100[1 - 0.125 \Sigma (|P\delta_{x,i} - P\delta_{y,i}| + |P\delta_{x,i} - P\varsigma_{y,i}| + |P\varsigma_{x,i} - P\delta_{y,i}| + |P\varsigma_{x,i} - P\varsigma_{y,i}|)]$$

where $P\delta_{x,i}$ and $P\varsigma_{x,i}$ are the proportions of males and females of size class x at the ith depth and $P\delta_{y,i}$ and $P\varsigma_{y,i}$ are the proportions of size class y at the ith depth within a habitat. Computation of α_{WS} is independent of the sex ratio in the population because size class proportions of males are calculated separately from females. If the occurrence of each size class is independent of sex, we would predict α_W to be equal to α_{WS}. If $\alpha_{WS} < \alpha_W$, then overlap within a habitat may be reduced by spatial separation of the sexes.

Results

Habitat Characteristics

Variations in substrate and macrophyte density were observed at different sampling locations and depths (Table 1). The shallow bays had a greater diversity of macrophytes than the deep bays and main basin, but *Myriophyllum* sp. and *Ceratophyllum demersum* were the dominant aquatic vascular plants at all locations. Temperature and oxygen profiles obtained from the middle of the lake in June and August were representative of values measured at each sampling location. Oxygen concentrations exceeded 8 mg/L at all locations in June. Water temperatures were less than 20°C. After stratification, the thermocline

TABLE 1. Characteristics of the three habitat types at depths sampled in Lake West Okoboji, 1981.

Habitat type	Depth (m)	Predominant substrate	Submersed aquatic macrophyte cover (%)
Main basin	2.5	Cobble/gravel	15–25
	5.0	Cobble/gravel	15–25
	10.0	Sand	0
	15.0	Silt	0
Deep bays	2.5	Gravel/sand/silt	50–60
	5.0	Gravel/sand/silt	50–60
	9.0	Silt/ sand	0
Shallow bays	2.5	Gravel/sand/silt	70–80

formed between 10 and 15 m. In August, water temperatures were greater than 20°C in the epilimnion. The oxygen profile was a clinograde curve with dissolved oxygen concentrations greater than 9 mg/L in the epilimnion and less than 2 mg/L in the hypolimnion.

Perch Distributions

Differences in CPUE were noted between depths and habitats (Table 2). The maximum CPUE in deep bays was at 5 m; the main basin maximum was at 10 m. Deep bay CPUE values were less than main basin values at similar depths (Wilcoxen's signed-ranks test, $P < 0.05$). The CPUE values at 2.5 m in Little Millers Bay were less than those from the adjacent deep bay, Millers Bay, and the main basin in June and less than those in the main basin, but greater than from the deep bay, in August (Jonchiere's test, $P < 0.05$). No fish were caught at 15 m in the main basin in August, evidently because of low dissolved oxygen concentrations at that depth. Statistical comparisons were not made between Little Emerson Bay, Emerson Bay, and the other three locations because they were sampled about 1 wk after the main basin, Millers Bay, and Little Millers Bay.

The size–frequency distribution of yellow perch samples varied among the three habitat types (Fig. 1). The main basin had higher proportions of large fish than did the deep and shallow bays during both sampling periods (Chi-square, $P < 0.05$). Fish were primarily 201–250 mm long in the main basin, but predominantly 126–200 mm long in shallow and deep bays. The mean length of main basin perch at 2.5, 5, and 10 m was greater than that of perch from a deep bay, Millers Bay, in both June (ANOVA, df = 377,1, $P < 0.01$) and August (ANOVA, df = 680,1, $P < 0.01$). Deep bays had a higher proportion of fish 151–200 mm long than did the shallow bays in early summer. But there was little difference between size distributions in the two habitat types during late summer after the

TABLE 2. Catch (number of perch in 10 m of net per hour) of monofilament gill nets in Lake West Okoboji, 1981 (LEB = Little Emerson Bay, LMB = Little Millers Bay, EMB = Emerson Bay, and MLB = Millers Bay).

		Season and location									
		Early summer					Late summer				
Depth (m)	Perch size class (mm TL)	LEB	LMB	EMB	MLB	Main basin	LEB	LMB	EMB	MLB	Main basin
2.5	126–150	12.0	1.0	1.5	1.5	0	16.0	1.0	13.0	0.5	0.5
	151–175	7.0	0.5	1.5	4.5	1.5	2.0	3.5	1.0	0.5	0.5
	176–200	4.0	1.5	1.5	4.5	0.5	3.0	2.0	8.3	0	1.5
	201–225	1.0	0	0	0.5	4.0	3.5	0.5	3.3	0.5	6.5
	226–250	1.0	0	0	0.5	6.5	0.5	0.5	2.7	2.0	3.5
	251–275	0	0	0	0	4.5	0	0	0	0.5	0
Total		25.0	3.0	4.5	11.5	17.0	25.0	7.5	28.3	4.0	12.5
5	126–150			0.5	5.0	1.0			16.5	13.5	9.5
	151–175			13.5	14.5	1.9			3.0	5.5	2.9
	176–200			5.0	9.0	4.3			4.5	4.5	22.6
	201–225			1.5	7.5	18.8			0.5	8.5	36.7
	226–250			0.5	4.0	12.3			0.5	6.2	17.3
	251–275			0	0.5	1.9			0	0.5	2.5
Total				21.0	40.5	40.2			25.0	38.7	91.5
9–10	126–150			3.5	0	0.5			2.2	10.0	21.0
	151–175			12.0	8.5	1.5			1.1	3.0	16.6
	176–200			2.5	6.0	7.5			0.5	5.3	21.3
	201–225			0.5	0.5	35.5			0	4.2	62.8
	226–250			0	4.0	13.0			0	2.7	38.6
	251–275			0	0	1.5			0	0	4.5
Total				18.5	19.0	59.5			3.8	25.2	164.8
15	126–150					0					0
	151–175					0.5					0
	176–200					0.5					0
	201–225					5.2					0
	226–250					2.3					0
	251–275					0.4					0
Total						8.9					0

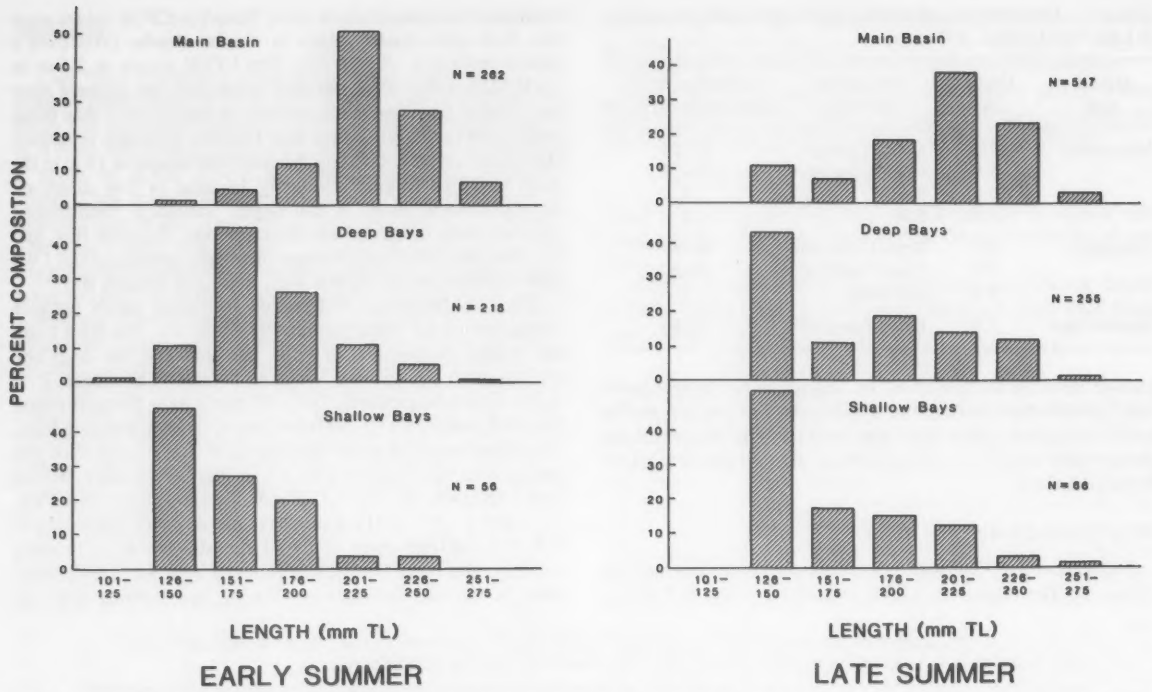

FIG. 1. Length–frequency distributions of yellow perch in samples from the main basin, deep bays, and shallow bays of Lake West Okoboji, summer 1981.

TABLE 3. Mean total length (mm) ± SE of yellow perch from sampling locations in Lake West Okoboji, 1981 (sample size is in parentheses; LEB = Little Emerson Bay, LMB = Little Millers Bay, EMB = Emerson Bay, MLB = Millers Bay).

	Shallow bays		Deep bays		Main
Depth (m)	LEB	LMB	EMB	MLB	basin
			Early summer		
2.5	158±4 (50)	168±12 (6)	157±9 (10)	176±5 (23)	230±5 (34)
5			176±3 (42)	184±3 (81)	218±3 (90)
9–10			161±3 (37)	184±3 (36)	215±2 (119)
15					221±5 (19)
All depths			168±4 (89)	183±4 (140)	219±3 (262)
			Late summer		
2.5	162±4 (51)	178±6 (15)	175±5 (58)	212±15 (8)	216±5 (25)
5			154±3 (50)	181±4 (79)	204±2 (194)
9–10			150±3 (7)	178±5 (53)	203±2 (327)
All depths			164±4 (115)	182±6 (140)	204±2 (546)

formation of the anoxic hypolimnion. Perch size classes were not distributed equally among different depths within specific habitats (Chi-square, $P < 0.05$), though only minor differences in mean total length occurred (Table 3).

Spatial overlap between size classes within main basin and deep bay habitats (α_W) was calculated for perch 101–250 mm long (Table 4). Values ranged from 36 to 98% at the three sites. Early summer median values were 70% for the main basin, 78% for Millers Bay, and 59% for Emerson Bay. Overlap increased in late summer with median values of 86% in the main basin, 87% for Millers Bay, and 76% for Emerson Bay.

Segregation of size classes into different habitats (α_B) was evident (Table 4). Overlap decreased with increased differences in perch length. Between-habitat overlap (α_B) was less than within-habitat overlap for similar size classes and habitats (Wilcoxen's signed-ranks test, $P < 0.05$). Between-habitat values increased in late summer, but were still less than comparable within-habitat values (Wilcoxen's signed-ranks test, $P < 0.05$).

The sex ratio of the samples changed with depth. Nearshore and shallow bay sites had a higher proportion of females than males. A significant positive correlation ($R = 0.73$, df = 24, P

TABLE 4. Median habitat overlap values for yellow perch size classes in Lake West Okoboji, 1981 (range of values is in parentheses).

Season and location	Within habitat (α_W)	Between sex (α_{WS})	Between habitat (α_B)
Early Summer			
Main basin	70 (41–93)	65 (61–87)	52 (22–83)
Millers Bay	78 (69–94)	71 (57–82)	
Emerson Bay	59 (36–89)	56 (30–78)	48 (17–86)
Late summer			
Main basin	86 (64–97)	77 (59–87)	73 (61–87)
Millers Bay	87 (70–98)	80 (72–85)	
Emerson Bay	76 (34–98)	65 (26–80)	56 (39–85)

< 0.01) occurred between sampling depth and the proportion of males in the sample during early summer (Fig. 2). Trends were similar at shallow and deep bay sites in late summer, but in the main basin the sex ratio was near unity at all depths. There was no significant difference in length between males and females at a specific depth, except at 5 and 9 m in Emerson Bay in early summer, and at 2.5 m in the main basin in August (t-test, $P < 0.05$); however, differences were less than 1 cm.

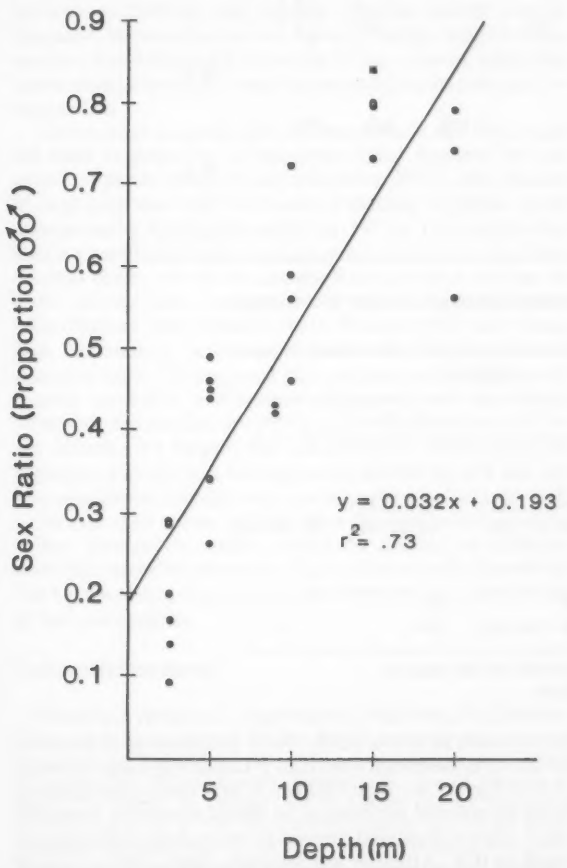

FIG. 2. Early summer sex ratio (proportion of males) versus depth in Lake West Okoboji. Data includes all sites and depths sampled in 1981 and 13 main basin depths sampled in June 1980 (unpubl. data).

Overlap between size classes within a habitat was reduced when sex differences in depth distribution were accounted for (Table 4). Sex overlap values (α_{WS}) in early and late summer were less than within-habitat values (Wilcoxen's signed-ranks test, $P < 0.05$).

Diet

The stomach contents of yellow perch varied with habitat type, depth, and sampling period (Table 5). Perch of all size classes ate similar food organisms at a specific depth within the main basin and Millers Bay. As perch size increased so did the number of taxa eaten by perch from the main basin. There appeared to be no trend in either the percentage of stomachs containing food or in the mean weight of stomach contents among different length classes of yellow perch.

Median values of early summer diet overlap (α) between size classes ranged from 64% at 10 m to 78% at 15 m in the main basin (Table 6). Overlap values in the deep bay showed similar trends, with median values at each depth being greater than 70%. Shallow bay perch, 101–175 mm long, exhibited 100% overlap in diet. But values decreased with increasing differences in size, and diet overlap was nonexistent between perch 101–175 mm and those 226–250 mm long.

Discussion

The segregation of yellow perch of different size classes into different habitats may be an important mechanism reducing niche overlap in Lake West Okoboji. Schmitt and Hubert's (1983) observations on the movements of yellow perch in the Okoboji lakes allow us to conclude that the patterns of spatial separation were not artifacts of distinct populations with unique size distributions in the different habitat types. Spatial segregation of conspecific size classes occurs in bluegills, *Lepomis macrochirus* (Keast 1977b; Hall and Werner 1977), pumpkinseeds, *L. gibbosus*, northern longear sunfish, *L. megalotis peltastes* (Laughlin and Werner 1980), and alewives, *Alosa pseudoharengus* (Brandt 1980), and may be a method of resource partitioning resulting from intraspecific competition (Keast 1978). In Lake Michigan, Brandt et al. (1980) found that perch of different size classes inhabited different thermal zones at various depths. Spatial separation of perch size classes by depth within a habitat was less important in Lake West Okoboji.

Length–frequency distributions and CPUE's indicated that small perch were most abundant in the dense littoral vegetation of shallow and deep bays. In contrast, large perch were most abundant at 5 and 10 m in the main basin, where macrophytes were sparse to nonexistent. Large perch may limit their distribution to areas of the lake where dense vegetation will not disrupt schooling behavior or reduce foraging efficiency by inhibiting prey location and capture. Field and laboratory studies with largemouth bass, *Micropterus salmoides* (Glass 1971), and bluegill (Crowder and Cooper 1979) suggest that a large predator's rate of prey capture is reduced with increased environmental structure. The restriction of small fish to the protective cover of dense vegetation has been interpreted as a response to predation or as a competitive refuge from large fish (Hall and Werner 1977; Werner et al. 1977; Mittelbach 1981a).

Spatial separation of the sexes may be a mechanism further reducing resource overlap in yellow perch. Females were most abundant in shallow areas, and males in deeper waters. Similar distributions have been observed in Lake Erie (Jobes 1952),

TABLE 5. Stomach contents (percent dry weight) of yellow perch from different locations and depths (m) in Lake West Okoboji, 1981 (diet analysis based on 321 stomachs sampled in early summer and 395 stomachs sampled in late summer).

	Locations and depth (m)							
	Main basin				Millers Bay			Little Emerson Bay,
Season and taxa	2.5	5	10	15	2.5	5	9	2.5
Early summer								
Cladocera	12.8	78.7	79.9	19.7	68.2	96.1	86.8	54.0
Amphipoda								
Hyalella azteca	76.8	10.3			1.6		0.2	
Odonata								
Enallagma sp.					2.1	0.2		
Anax sp.					28.1			
Ephemeroptera								
Caenis sp.	0.2	2.9	0.2			0.5		
Hexagenia sp.		Trace						
Trichoptera								
Leptocercus sp.	2.1	0.4			Trace		0.2	
Gastropoda								
Physa sp.						3.0		
Diptera								
Chironomus sp.			14.4	79.0			8.4	
Procladius sp.		1.9					2.6	
Cryptotendipes sp.	3.2	6.2	5.5	0.5		0.1	1.7	
Microspectra sp.	1.1							
Pisces								46.0
Late summer								
Cladocera	85.0	99.0	100		100	100	100	
Decapoda								
Orconectes sp.	13.1							16.2
Ephemeroptera								
Hexagenia sp.		1.0						
Pisces	1.8							83.8

TABLE 6. Median diet overlap values for yellow perch size classes in Lake West Okoboji, 1981 (range of values is in parentheses).

	Depth (m)			
Season and location	2.5	5	9–10	15
Early summer				
Little Emerson Bay	15 (0–100)			
Millers Bay	91 (91–94)	95 (91–100)	73 (62–92)	
Main basin	70 (59–63)	66 (27–99)	64 (51–89)	78 (68–92)
Late summer				
Little Emerson Bay	69 (38–100)			
Millers Bay	—[a]	100	100	
Main basin	100	100 (0–100)	100	—[b]

[a]Overlap not calculated. Only one size class available for diet analysis.
[b]No fish caught at 15 m due to anoxic hypolimnion.

Lake Michigan (Wells and Jorgenson 1983), and several Michigan lakes (Eschmeyer 1937, 1938), but the sex ratio of yellow perch has not been previously correlated with depth. Sexual differences in temperature preference may account for the correlation. Females of the Ozark minnow, *Notropis nubilus* (Baker et al. 1970), and of several species of Poeciliidae (Gibson 1954; Tsukuda 1960; Hagen 1964) have higher temperature tolerances than do males. Ferguson (1958) suggested that a differential sex response to temperature may also be important in yellow perch. Water temperatures at depths of 10 and 15 m were often more than 3° cooler than temperatures at 2.5 and 5 m in Lake West Okoboji. A large temperature gradient is not an essential prerequisite for spatial separation. European perch (*Perca fluviatilis*) respond to temperature differences as small as 0.2° (Alabaster and Downing 1966). This degree of sensitivity supports the concept, proposed by Magnuson et al. (1979), that temperature must be considered as an ecological resource.

Male yellow perch are commonly smaller than females in this lake (Schmitt 1981) and other coolwater lakes. Lower metabolic rates, associated with cooler water temperatures found in deep water, may partly account for the slower growth rates and body size of males compared with females of the same age.

Food partitioning did not occur extensively between size classes of yellow perch in Lake West Okoboji. Our results are different from those of Keast (1977a), who studied yellow perch in the littoral zone of Lake Opinicon, Ontario, where diets of perch shifted with size. Studies by Parsons (1950), Scott (1955), Seaburg and Moyle (1964), and Clady (1974) also indicate that the diet of perch progressively shifts with growth from zooplankton to macroinvertebrates to fish.

Studies in other freshwater systems indicate that overlap is inversely related to competition (Nilsson 1960; Seaburg and Moyle 1964; Zaret and Rand 1971; Keast 1977a; Werner and Hall 1979). But in Lake West Okoboji, resource overlap increased in late summer after the formation of an anoxic hypolimnion. The increase in overlap occurred during a period in which macroinvertebrate densities are low in temperate lakes (Anderson and Hooper 1956; Mittelbach 1981b), the metabolic demands of the fish are high (MacLean and Magnuson 1977), and the habitat available to the perch was reduced to those areas above the thermocline. This suggests a positive relationship between competition and overlap. Though habitat overlap increased, between-habitat overlap and overlap between sexes was less than within-habitat overlap in late summer, indicating spatial segregation to be a mechanism reducing the potential for competition.

The presence of ample prey of intermediate and large sizes has been suggested as an important factor required for fast growth of perch (MacLean and Magnuson 1977). The absence of large prey was cited as a cause of stunting in yellow perch populations by Alm (1946) and Keast (1977a). Diet overlap was high and zooplankton was the main prey in the diet of Lake West Okoboji perch, yet fish in this population grow at average to above average rates, compared with growth of perch in other lakes (Parsons 1950; Schmitt 1981). Persson (1983) also found high diet overlap in European perch inhabiting a shallow, eutrophic lake. He proposed that pronounced habitat homogeneity prevented perch from segregating on the habitat dimension and resulted in a poorly growing population with few age classes. We suggest that the ability of yellow perch to segregate spatially into heterogeneous habitats by size and sex may compensate for high food overlap and the lack of large prey in the diet. The failure of Lake West Okoboji yellow perch to reduce intraspecific niche overlap by feeding on different taxonomic and size categories of prey reinforces the hypothesis that habitat partitioning is more important than food partitioning in fish communities.

Acknowledgements

We thank G. Atchison, P. Angermeier, R. Bachmann, K. Carlander, and an anonymous reviewer for their helpful comments and constructive criticisms. T. Gengerke and L. Mitchell reviewed an early draft of this manuscript. We are especially grateful to D. Long, D. Mozena, J. Miller, M. Parsley, R. Gardner, and M. Lannoo for their help in the field and laboratory. D. Cox assisted with statistical analysis. M. Wiley identified the chironomid larvae and J. Peck provided us with information on macrophyte densities in the lake. We also thank R. Bovbjerg, M. Wehrspann, and J. Wehrspann for providing laboratory facilities and assistance at Iowa Lakeside Laboratory. We gratefully acknowledge R. McWilliams, J. Christianson, and others associated with the Iowa State Conservation Commission at Spirit Lake, Iowa, for their advice and use of equipment. This study was funded by the Iowa State Conservation Commission.

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Size at Maturity for Northwest Atlantic Redfishes (*Sebastes*)

I-H. Ni and E. J. Sandeman

Department of Fisheries and Oceans, Fisheries Research Branch, P.O. Box 5667, St. John's, Nfld. A1C 5X1

Ni, I-H., and E. J. Sandeman. 1984. Size at maturity for Northwest Atlantic redfishes (*Sebastes*). Can. J. Fish. Aquat. Sci. 41: 1753–1762.

Morphological differences in Northwest Atlantic redfishes (*Sebastes*) are recognized but their biology is relatively unknown, due to the confusion associated with redfish systematics in past decades. For a redfish reproductive biology study we utilized historical sex and maturity data collected between 1957 and 1969. We applied the logistic model to estimate the size at maturity from 4501 *S. marinus* and 43 988 beaked redfishes (*S. mentella* and *S. fasciatus* combined) covering the whole Northwest Atlantic. The sizes at maturity for female redfishes were significantly larger than that of males for both *S. marinus* and beaked redfishes. The size at maturity in female *S. marinus* was significantly larger than that of beaked redfishes whereas in males there was no significant difference between groups. A geographic cline in size at maturity was noted in beaked redfishes, with a decreasing trend for *S. mentella* from Baffin Bay southward to the Gulf of St. Lawrence, and for *S. fasciatus* from the Grand Bank to the Nova Scotian Shelf.

Nous savons que les sébastes (*Sebastes*) du nord-ouest de l'Atlantique présentent des différences morphologiques, mais la biologie de ces poissons est relativement mal connue, car leur classification est restée confuse au cours des dernières décennies. Pour étudier la reproduction de la sébaste, nous avons employé des données d'archives portant sur le sexe et la maturité de 1957 à 1969. Nous nous sommes servi du modèle logistique pour estimer la taille à maturité de 4501 *S. marinus* et de 43 988 *S. mentella* et *S. fasciatus* pour l'ensemble de la région du nord-ouest de l'Atlantique. Chez toutes les espèces considérées, la taille des femelles à maturité était supérieure, dans une mesure significative, à celle des mâles. Par ailleurs, la taille à maturité des *S. marinus* femelles était supérieure de façon significative à celle des autres types de sébastes ; il n'y avait pas de différence significative entre les mâles. Chez *S. mentella* et *S. fasciatus*, nous avons constaté que la taille à maturité varie suivant une cline géographique : en effet, la taille de *S. mentella* tend à diminuer depuis la baie de Baffin jusqu'au golfe du Saint-Laurent, tandis que celle de *S. fasciatus* décroît depuis Grand Bank jusqu'au plateau continental de Scotian.

Received February 17, 1984
Accepted August 22, 1984
(J7693)

Reçu le 17 février 1984
Accepté le 22 août 1984

Redfish (*Sebastes*) compose the second largest groundfish nominal catch in the Northwest Atlantic (Northwest Atlantic Fisheries Organization 1983). However, the biological study of Northwest Atlantic redfishes has been hampered for decades by the confusion of the classification and nomenclature of *Sebastes* spp. Templeman and Sandeman (1957) pointed out two distinct "types" of redfish in the Northwest Atlantic. Specimens classified as the "mentella-type" or "beaked" redfish are bright red with a well-developed long pointed chin and relatively large eyes whereas those classified as "marinus-type" or "golden" redfish are orange or yellowish red with a poorly developed protrusion on the lower jaw and small eyes. This situation was further complicated when Barsukov (1968) recognized two species of beaked redfishes off eastern North America: *S. mentella* and *S. fasciatus*. Morphological differences among redfishes were then described by Barsukov (1972), Barsukov and Zakharov (1972), Litvinenko (1974), Templeman (1976, 1980), Ni (1981a, 1981b, 1981c), and Misra and Ni (1983). Until recently some opinions were that these morphological differences merely reflect geographic variation within the same species (Northwest Atlantic Fisheries Organization 1981). Studies of morphology of extrinsic gasbladder musculature (Litvinenko 1980; Ni 1981d; Power and Ni 1982) and biochemical population genetics (Payne and Ni 1982; McGlade et al. 1983) have substantiated the existence of the three genetically distinct redfish species. From studies of meristic patterns, Ni (1982, 1984) suggested where each redfish species was distributed in the Northwest Atlantic. Biological studies of these sibling redfish species were often confused because the species were mixed and thus were of reduced value.

The size at maturity is an important biological parameter for both reproduction and growth because, after the onset of maturity, energy that might have been used for growth will be diverted for gonad maturation and, in some cases, for making spawning migrations (Holt 1962). This population parameter might also be an indicator for species differentiation and stock discrimination, particularly for sibling redfish species and/or stocks. Therefore, we examined historical data to document the size at maturity of redfishes in the Northwest Atlantic and to investigate the differences in this vital statistic among redfish species.

Materials and Methods

Sex and maturity data for 4501 *S. marinus* and 43 988 beaked redfishes (*S. mentella* and *S. fasciatus* combined) were collected from Baffin Bay southward to the southern slope of the

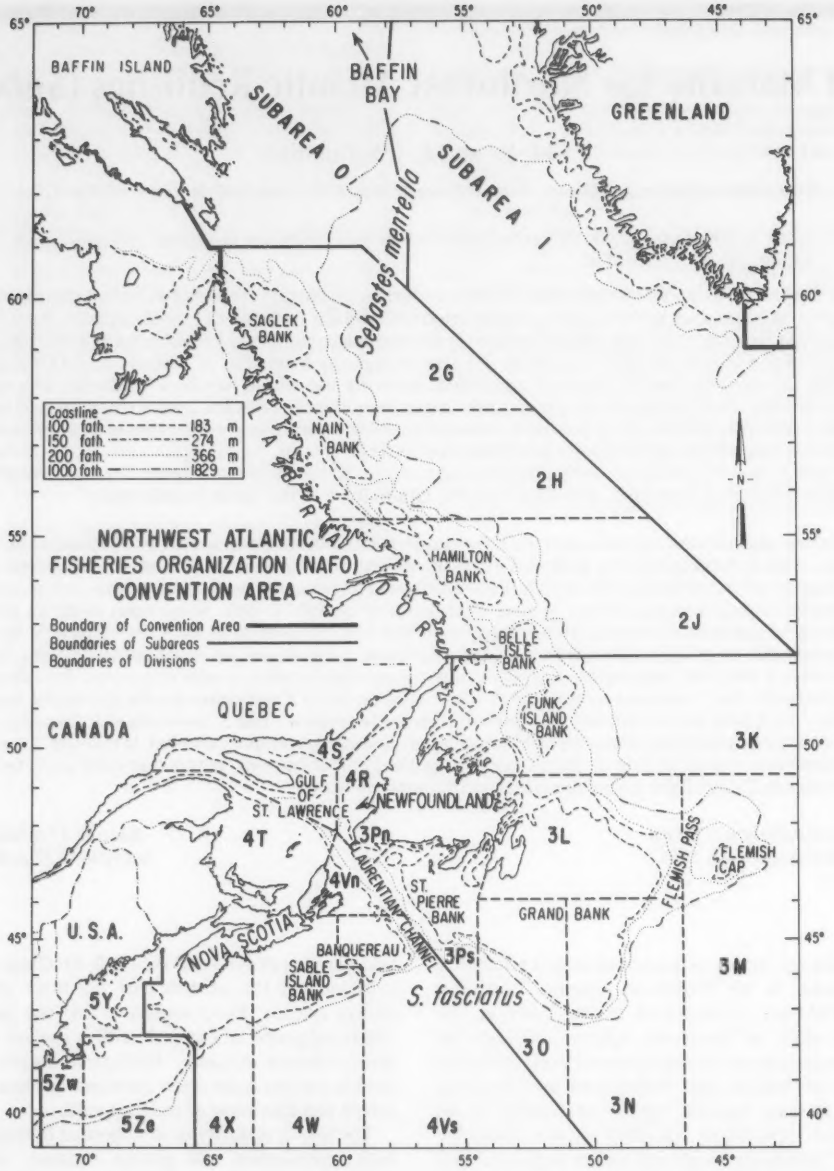


FIG. 1. NAFO Divisions and place names referred to in the text. Sample sites were along the continental slope at bottom depth around 100–750 m.

Grand Bank and westward off southern Newfoundland to the Gulf of St. Lawrence as well as the Nova Scotian Shelf (NAFO Div. 0-4X in Fig. 1) between 1957 and 1969 (Table 1). Sample sites were mainly along the continental slopes at bottom depths from 100 to 750 m. All analyses were conducted for two groups: *S. marinus* and beaked redfishes.

From microscopic examination of many testes, taken from small redfish throughout the year and especially during the season when the testes of mature male redfish might be expected to contain sperm, we suggest that if the testes were translucent, stringlike, and with widths less than 1 mm then the fish could be considered as immature. From similar microscopic examination in which the egg sizes of female redfish of different lengths were examined, we suggest that if there was no evidence of previous spawning (e.g. thicker gonad wall, no old eye pigment) and the eggs were smaller than 0.2–0.3 mm in diameter then the females could be considered as immature. Fish that did not meet these criteria were considered as mature (Ni and Templeman 1982).

Fork lengths of redfish (from the most anterior part of the lower jaw with the mouth closed to the middle rays of the caudal fin) were measured to the nearest centimetre. We grouped the

fish in 5-cm groups for length frequency analysis and in 2-cm groups for estimating size at maturity.

Fork length versus proportion mature for each sex were then plotted in each NAFO division. The sigmoid shape seemed to conform to a logistic equation, as applied to Pacific ocean perch (*S. alutus*) by Gunderson (1977), of the form (Ashton 1972)

$$(1)\quad P = \frac{1}{1 + e^{-(\alpha+\beta L)}} \quad \text{or} \quad \frac{e^{\alpha+\beta L}}{1 + e^{\alpha+\beta L}}$$

where P = estimated proportion for mature fish, L = fork length (centimetres), and α and β = coefficients. The logit, a contraction of the phrase "logistic unit" or "log odds," is given by

$$(2)\quad \text{logit } P = \ln \frac{P}{1-P} = \alpha + \beta L.$$

The size at maturity (L50) is defined as the length at which 50% of the fish are in the mature stage. Because the logistic curve is symmetrical, the area under the curve and to the left of L50 is equal to the area above the curve and to the right of it. Hence, the errors introduced by assuming knife-edged maturation at L50 tend to balance.

The BMDPLR program (Engelman 1981) calculated the observed mature proportion, its predicted probability, and coefficients of the logistic equation. Thus, the size at maturity could be estimated as the negative ratio of coefficients (i.e. $-\alpha/\beta$) by substituting $P = 0.5$ in equation (2).

To examine the differences of size at maturity among areas, we calculated the sample variance of L50 from the variance and covariance of coefficients α and β (Ashton 1972):

$$(3)\quad S^2(\text{L50}) = \frac{1}{\beta^2}\left[S^2(\alpha) + \frac{\alpha^2}{\beta^2} S^2(\beta) - \frac{2\alpha}{\beta}\text{cov}\,(\alpha, \beta)\right].$$

Results

Sex Ratio

By examining the reproductive cycles of the ovoviviparous redfish, Magnusson (1955) noted that the European male and female redfish were almost completely separated in certain seasons, especially from the end of copulation until the extrusion of the larvae. Sorokin (1964) also reported that the immature and mature redfish live in different European waters and the sexes are separated when the fishery is most intense. Therefore, the sex ratio might serve as an important character for the homogeneity of the redfish population, and also as a good indicator of possible migrations. The sex ratios (male to female) were around 1 and ranged from 0.77 (Div. 3O) to 1.30 (Div. 3M) for beaked redfishes and from 0.71 (Div. 2J) to 1.33 (Div. 3P) for *S. marinus* (Table 1). The lack of seasonal sampling in the past and the large size of NAFO Divisions made the interpretation difficult. However, the number of males equals the number of females from all areas combined for both beaked redfishes and *S. marinus*.

Size Composition

Percentage length frequencies for both beaked redfishes (Fig. 2) and *S. marinus* (Fig. 3) are displayed from each NAFO Division. Males and females are treated separately because Templeman (1959) suggested that differences in sex ratio are often due to the unavailability of mature females. No calculation could be conducted for *S. marinus* in Div. 2GH and 4STVWX due to lack of specimens (Ni and McKone 1983).

TABLE 1. Sample size and sex ratio of *S. marinus* and beaked redfishes (*S. mentella* and *S. fasciatus*) in NAFO Divisions. Numbers in parentheses are small sample sizes.

NAFO Div.	Beaked redfishes		*S. marinus*	
	N	Sex ratio male/female	*N*	Sex ratio male/female
0	776	0.86	(13)	(0.44)
1	596	1.11	136	0.81
2G	468	1.28	0	—
2H	1 057	0.96	(1)	—
2J	3 998	1.09	1037	0.71
3K	3 351	0.98	424	1.29
3M	2 689	1.30	737	1.21
3L	2 127	1.13	74	0.76
3N	2 570	1.03	190	0.98
3O	2 496	0.77	53	1.12
3P	9 591	0.94	1809	1.33
4R	5 422	1.0	(26)	(1.89)
4S	2 172	1.17	0	—
4T	1 673	1.05	(1)	—
4V	1 080	0.82	0	—
4W	2 710	0.90	0	—
4X	1 212	0.89	0	—
Total	43 988	1.08	4501	0.99

In general, the females were relatively larger than the males in both groups of redfishes, and *S. marinus* were much larger than beaked redfishes (except Div. 3L). The smaller size classes of *S. marinus* were seldom recorded because morphological characters used in differentiating redfishes may not be well defined in specimens <20 cm (Templeman and Sandeman 1957; Power and Ni 1982).

In Baffin Bay (Subarea 0 and 1), mature females could rarely be found for either *S. marinus* or beaked redfishes even for very large size specimens (70 cm in *S. marinus* and 45 cm in beaked redfishes). However, mature males were noted in specimens with size larger than 30 cm for *S. marinus* and 20 cm for beaked redfishes, respectively. In Northern Labrador (Div. 2GH) a larger proportion of mature males (>25 cm) of beaked redfishes were encountered whereas females were mainly in the immature stage. Mature fish were dominant in Southern Labrador (Div. 2J) for *S. marinus* (>25 cm in males and >35 cm in females) and for male beaked redfishes (>20 cm), but the immature females of beaked redfishes were still abundant. From northeastern Newfoundland waters (Div. 3K) southward to the Nova Scotian Shelf (Div. 4VWX), proportion mature of the same size range gradually increased toward the south.

Size at Maturity

For beaked redfishes and *S. marinus*, the fork length versus proportion mature were plotted for each sex and NAFO Division (Fig. 1). The logistic equation was computed to estimate the parameters (coefficients α and β) and predicted probability of mature fish. The theoretical curve is also presented (Fig. 4). The size at maturity (L50) and its standard error (SE) were then calculated and listed with sample size and proportion mature (Table 2). Interpretation of size at maturity should be cautious if the sample size is small and the numbers of immature or mature specimens insufficient.

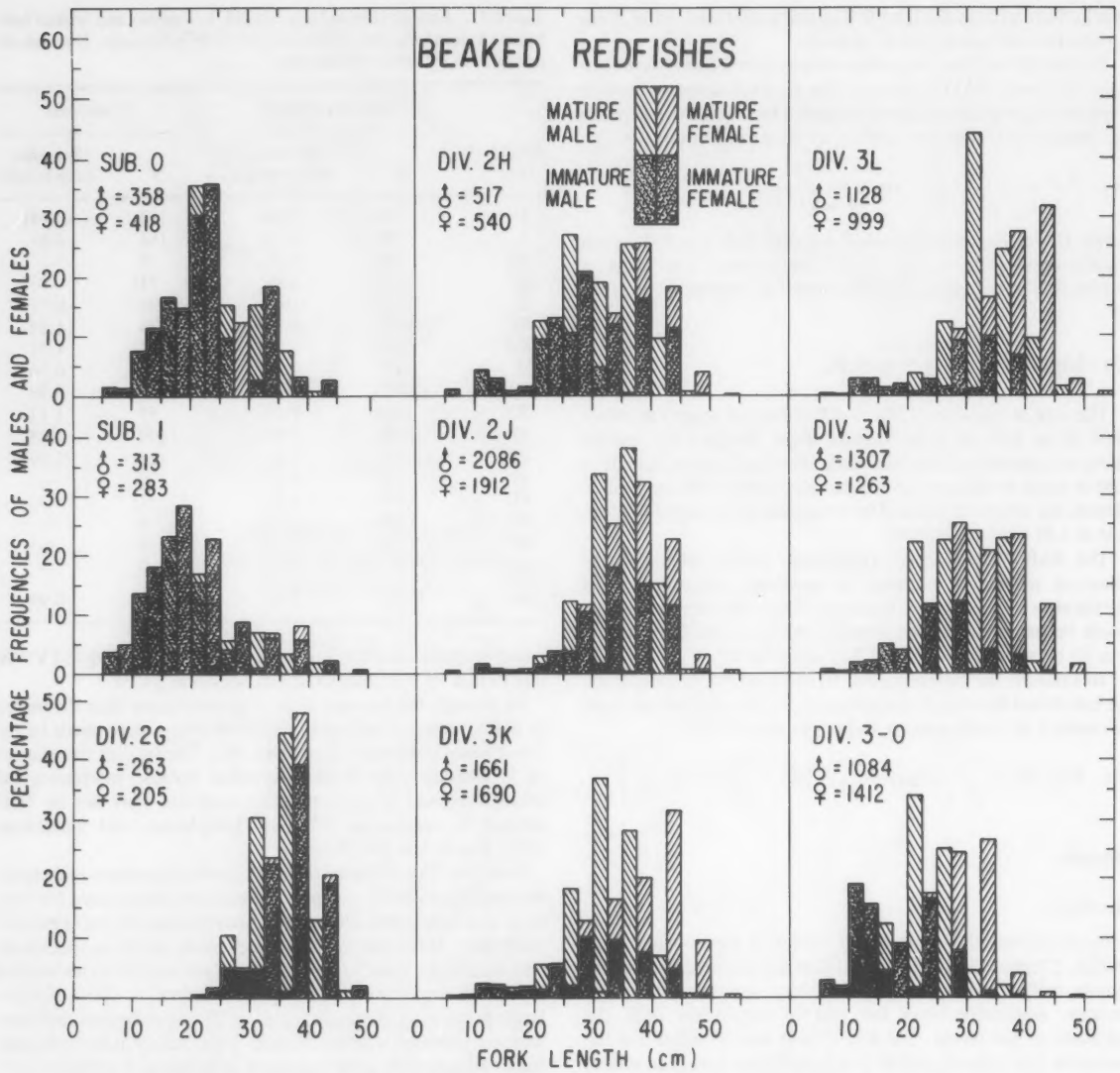


FIG. 2. Length frequency distribution with proportion mature by sex for beaked redfishes in NAFO Divisions.

The sizes at maturity for female redfish were significantly larger than those of males for both beaked redfishes and *S. marinus* in every NAFO Division sampled (Fig. 5). Significant differences in size at maturity in females between beaked redfishes and *S. marinus* were observed in Div. 2J to 4R (Fig. 5). The males, however, usually did not show a significant difference in size at maturity between groups.

The usage of L50 to describe maturity size can be verified by the display of the coefficient β and the standard error in Table 2. A better representation of L50 would be encountered if the coefficient β is large (i.e. sharp steepness of logistic curve) and the standard error small. However, the small β value with large standard error value for beaked redfishes may be due to a mixture of *S. mentella* and *S. fasciatus*, if the sample size is sufficient.

A geographic cline in size at maturity was observed in beaked redfishes: it gradually decreased from 29.14 cm in Subarea 0 and 29.45 cm in Subarea 1 down to 15.96 cm in Div. 4X for males and from 43.14 cm in Div. 2H down to 25.96 cm in Div. 4X for females (Fig. 5). However, except for the males in Div. 2J, *S. marinus* displayed less geographic variation in size at maturity.

Discussion

The redfish described in this paper were identified following

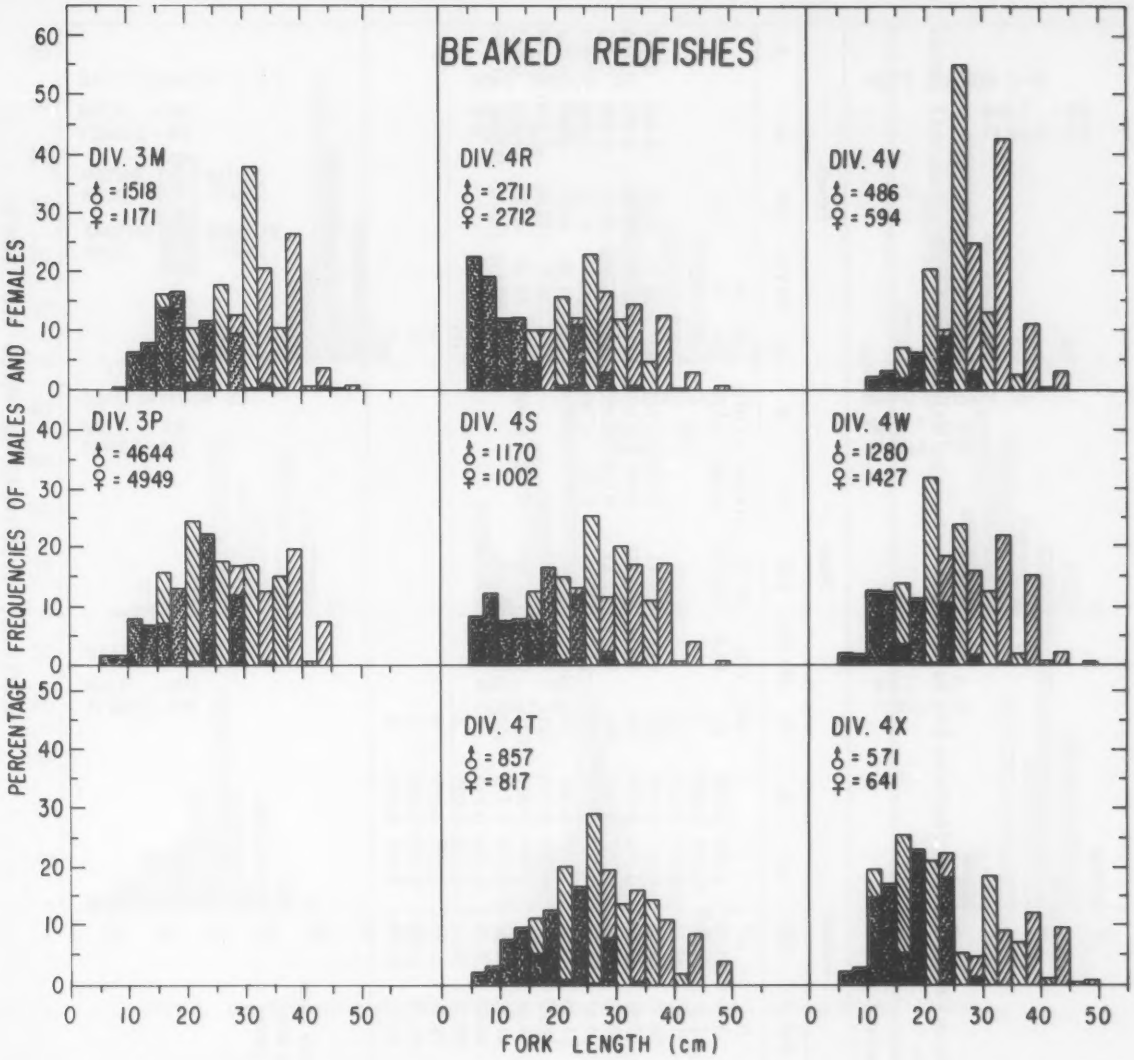


FIG. 2. (*Concluded*)

the criteria of Templeman and Sandeman (1957). A possible misjudgement in classification was the misplacement of the small sized (<20 cm) *S. marinus* into beaked redfishes. Fortunately, *S. marinus* only contribute a minor portion of total redfish catches (Ni and McKone 1983), and the very large sample size of beaked redfishes is not likely to be biased by a small number of misclassified *S. marinus* in the estimation of size at maturity.

The adequacy of the length–maturity relationship as described by the logistic model varied with area. Generally speaking, the data base suffered from insufficient mature females in northern waters (Subareas 0 and 1, Div. 2G and 2H) or from the difficulties in identification of immature male *S. marinus*. However, a trend of the differences between the observed and predicted proportion mature could be gathered by comparing redfish species distribution (Ni 1982, 1984; Ni and McKone 1983). For beaked redfishes the logistic curve fitted notably better in the Davis Strait (Subareas 0 and 1) as well as in the Gulf of St. Lawrence (Div. 4RST), since *S. mentella* was the dominant species. This was also observed on the Nova Scotia Shelf (Div. 4VWX) and in southern Newfoundland waters (Div. 3P in Ni and Templeman 1982, fig. 3) where *S. fasciatus* was predominant (Power and Ni 1982). Unsatisfactory compliance with the model was observed in southern Labrador waters (Div. 2J), in northeastern Newfoundland waters (Div. 3K), and on the Flemish Cap (Div. 3M), where two beaked redfish species were encountered. A slight improvement of the fit was noted on the Grand Bank (Div. 3LNO), where a mixture of *S. fasciatus* and *S. mentella* occurred only in deep waters.

No mature female redfishes were observed in the Davis Strait

TABLE 2. Proportion mature (PM), size at maturity (L50 in cm with SE), and estimated coefficie
Interpretation of numbers in parentheses should be cautious.

NAFO Div.	Beaked redfishes (*S. mentella* and/or *S. fasciatus*)									
	Male					Female				
	N	PM (%)	L50	SE	β	*N*	PM (%)	L50	SE	β
0	358[a]	31.29	29.14	0.465	0.389	418[a]	0	—[f]		
1	313[a]	17.89	29.45	0.620	0.501	283[a]	3.5	(45.09)[h]	2.495	0.229
2G	263[a]	89.35	29.01	0.802	0.425	205[a]	11.7	(59.69)[h]	12.679	0.095
2H	517[a]	68.09	27.68	0.461	0.278	540[a]	21.85	43.14	0.684	0.230
2J	2086[b]	90.84	24.93	0.483	0.330	1912[b]	38.76	40.57	0.397	0.145
3K	1661[b]	92.72	20.80	0.582	0.309	1690[b]	57.63	35.88	0.301	0.233
3M	1518[c]	77.54	21.47	0.215	0.550	1171[c]	50.30	30.61	0.252	0.460
3L	1128[d]	92.64	21.80	0.667	0.330	999[d]	65.17	34.65	0.315	0.302
3N	1307[d]	95.33	16.32	0.709	0.362	1263[d]	63.10	29.58	0.271	0.303
3O	1084[d]	72.97	18.23	0.218	0.686	1412[d]	48.02	27.73	0.136	0.756
3P	4643[d]	82.55	18.56	0.095	0.809	4948[d]	44.06	29.61	0.090	0.804
4R	2711[c]	60.24	18.71	0.152	0.726	2711[c]	44.72	26.60	0.134	0.773
4S	1170[c]	75.64	19.23	0.239	0.615	1002[c]	48.60	26.89	0.250	0.810
4T	857[c]	83.90	18.77	0.263	0.776	816[c]	50.37	28.12	0.178	0.925
4V	486[e]	96.09	17.40	0.307	1.460	594[e]	78.79	26.36	0.259	0.958
4W	1283[e]	81.92	17.37	0.180	1.010	1427[e]	61.53	24.44	0.189	0.599
4X	571[e]	77.76	15.96	0.246	0.691	641[e]	38.22	25.96	0.380	0.590

[a] *S. mentella*.
[b] Mixture of *S. mentella* and *S. fasciatus*.
[c] *S. mentella* dominant with some *S. fasciatus* from shallow water.
[d] *S. fasciatus* dominant with some *S. mentella* from deep water.
[e] *S. fasciatus* dominant with few *S. mentella* from deep water.
[f] No immature or mature fish, no estimate can be made.
[g] Small sample size, interpretation should be cautious.
[h] Insufficient number of mature fish.
[i] Insufficient number of immature fish.

coefficient β for the logistic equation by sex and NAFO Division in beaked redfishes and *S. marinus*.

	S. marinus									
	Male					Female				
β	*N*	PM (%)	L50	SE	β	*N*	PM (%)	L50	SE	β
	(4)[g]	(75)	(52.35)	(118.94)	(1.051)	(9)	0	—[f]		
0.229	61	95.0	(40.76)[i]	4.694	0.21	75	0	—[f]		
0.095	0					0				
0.230	(1)	—[f]				0				
0.145	430	97.67	26.43	0.726	0.748	607	89.79	38.19	0.469	0.657
0.233	239	99.16	(21.13)[i]	0.937	3.389	185	87.03	38.15	0.921	0.604
0.460	404	94.55	22.23	0.958	0.362	333	56.46	39.21	0.490	0.402
0.302	32	81.25	21.15	0.910	0.794	42	16.67	41.21	2.335	0.309
0.303	94	100	—[f]			96	39.58	40.57	0.590	0.528
0.756	(28)	96.43	—[i]			(25)	(16.0)	(39.01)	(0.324)	(6.494)
0.804	1031	99.71	(16.95)[i]	5.778	0.304	778	49.10	40.32	0.233	0.513
0.773	(17)	100	—[f]			(9)	(88.89)	(40.51)	(43.18)	(1.468)
0.810	0					0				
0.925	0					(1)				
0.958	0					0				
0.599	0					0				
0.590	0					0				

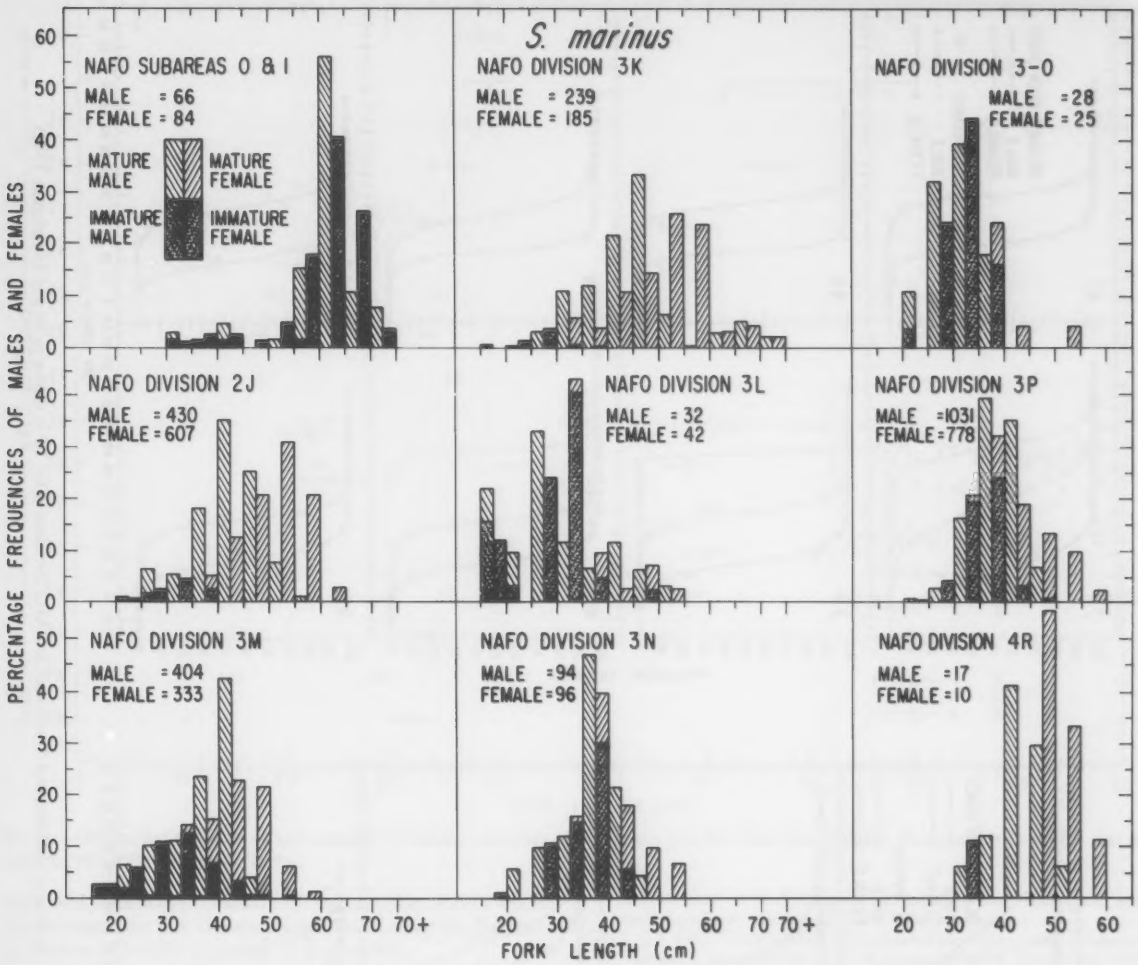


FIG. 3. Length frequency distribution with proportion mature by sex for *S. marinus* in NAFO Division.

(NAFO Subareas 0 and 1), with a negligible 3.5% proportion mature of *S. mentella* in West Greenland (Subarea 1). Also, a greater number of females than males was noted with the exception of *S. mentella* in West Greenland. Travin and Pechenik (1962) proposed that the immature *S. marinus* off Western Greenland (Subarea 1) were supplemented by young from the spawning grounds of Iceland and the Denmark Strait. The variation of sex ratios from area to area may indicate that the Northwest Atlantic redfishes are migratory species, as noted by Sorokin (1960) for the European redfish.

With regard to the differences in reproductive biology among redfish species, there appears to be no significant difference in size at maturity between male *S. marinus* and male beaked redfishes. However, there were significant differences in females. A decreasing trend in size at maturity from north to south was noted in beaked redfishes. This "clines" seems to be related to both species composition and geographic distribution. This inference was drawn because (a) *S. mentella* dominated in northern areas (Subareas 0 and 1, Div. 2G and 2H) whereas *S. fasciatus* dominated in southern areas (Div. 3LNOP and Div. 4VWX) (Ni 1982) and (b) the size at maturity of *S. mentella* in Baffin Bay (Subareas 0 and 1) and Northern Labrador waters (Div. 2G and 2H) is significantly greater than that of *S. mentella* in the Gulf of St. Lawrence (Div. 4RST) (Fig. 1; Table 2). Also, the L50 of *S. fasciatus* on the Grand Bank (Div. 3LNO) and St. Pierre Bank (Div. 3P) is greater than the L50 of *S. fasciatus* on the Nova Scotian Shelf (Div. 4VWX). Interestingly, this geographic variation of size at maturity in beaked redfishes was somewhat different from the geographic cline noted with meristics (Ni 1984). The difference was that the meristics

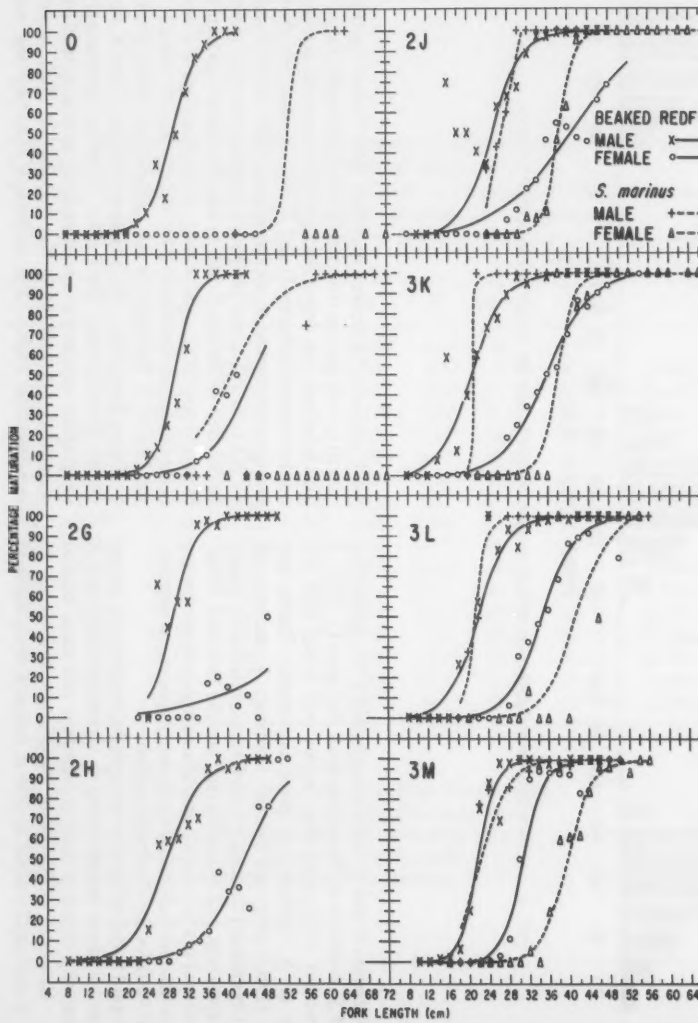
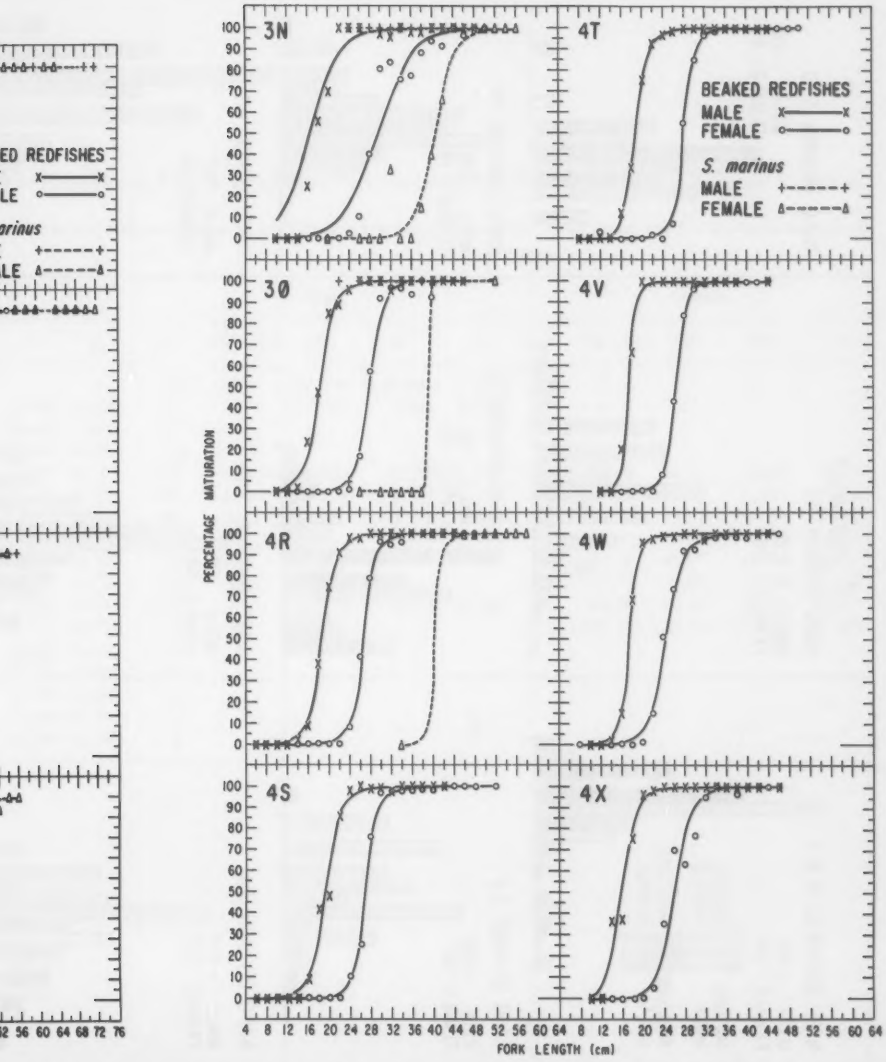


FIG. 4. Proportion mature versus fork length by sex for beaked redfish



ed redfishes and *S. marinus* in NAFO Divisions (Div. 3P is shown in Ni and Templeman 1982).

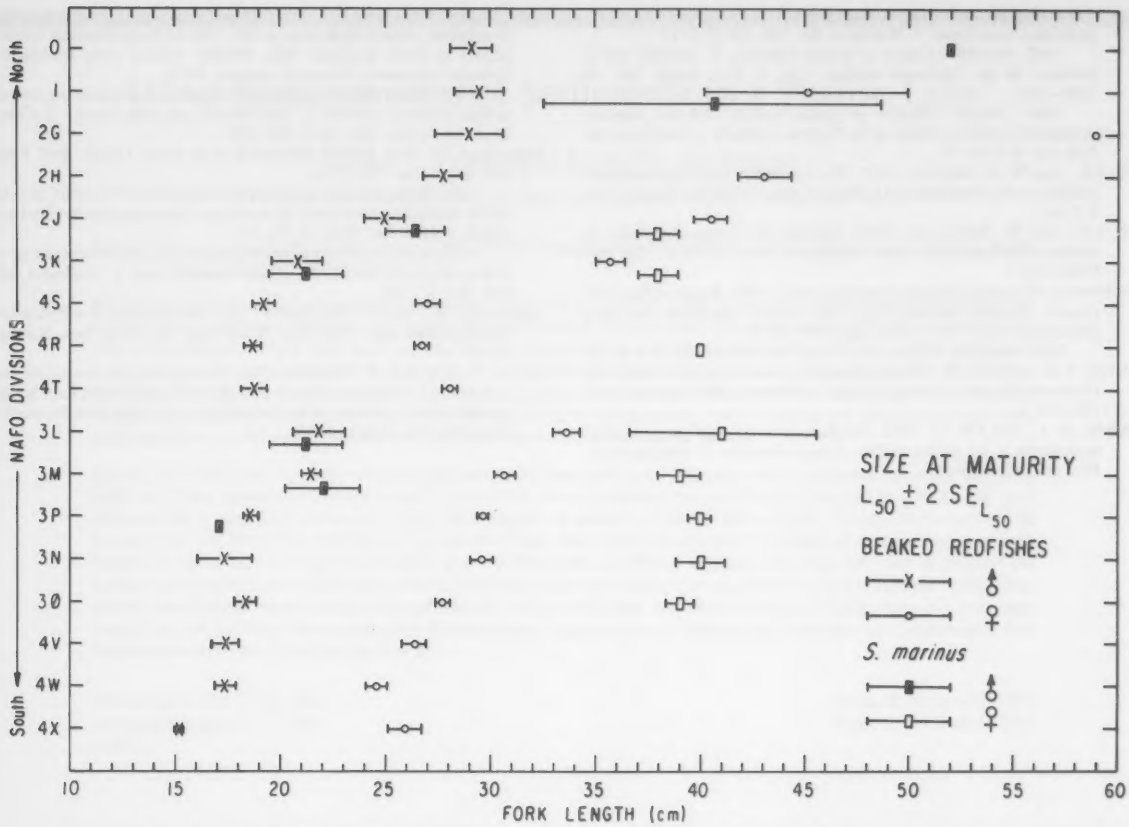


FIG. 5. Geographic variation of size maturity for beaked redfishes and *S. marinus* in the Northwest Atlantic. Horizontal bars are the size at maturity with 95% confidence limits.

decreased from north to south (with an exception on the Flemish Cap) whereas the size at maturity decreased along the continental shelves of NAFO Divisions (Fig. 1 and 5).

Acknowledgments

We are grateful to W. Templeman for the privilege of using previously collected data, the redfish section staff who contributed the sampling, C. B. Bourgeois and D. J. Power for assembling the figures, and C. I. Lee, G. T. Evans, D. B. Atkinson, G. R. Lilly, and A. T. Pinhorn for their valuable comments.

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Wind Resuspension of Sediments in a Prairie Lake[1]

Glenn L. Carper and Roger W. Bachmann

Department of Animal Ecology, Iowa State University, Ames, IA 50011, USA

Carper, G. L., and R. W. Bachmann. 1984. Wind resuspension of sediments in a prairie lake. Can. J. Fish. Aquat. Sci. 41: 1763–1767.

We measured levels of inorganic suspended solids in Little Wall Lake, Iowa, and concluded that sediment resuspension occurred when wind velocities exceeded critical velocities as calculated from wave theory. The percentages of the lake bed subject to resuspension for winds of given velocities were calculated, as were the percentages of time that winds of such velocities could be expected. We concluded that only a small percentage of the lake bed is subject to resuspension most of the time. The techniques to calculate wind effects and to summarize the data on frequency of wind mixing used in this study should be generally applicable to problems of sediment resuspension in other shallow lakes.

Après avoir mesuré la concentration de particules inorganiques en suspension dans les eaux du lac Little Wall en Iowa, nous avons conclu qu'il y a remise en suspension des sédiments lorsque la vitesse du vent dépasse une certaine valeur critique, déterminée d'après la théorie des vagues. Nous avons calculé la proportion du lit du lac remise en suspension par des vents de diverses vitesses et déterminé pendant combien de temps on peut s'attendre que de tels vents soufflent. Nous avons constaté que la plupart du temps seulement une faible proportion du fond du lac est remise en suspension. Les méthodes que nous avons employées pour calculer les effets du vent et résumer nos données sur la fréquence du brassage sous l'action du vent devraient être généralement applicables à l'étude de la remise en suspension des sédiments dans les lacs peu profonds.

Received January 10, 1984
Accepted August 30, 1984
(J7654)

Reçu le 10 janvier 1984
Accepté le 30 août 1984

The resuspension of sediments by wave action is a mechanism that can lead to temporary increases in turbidity and enhance nutrient cycling by bringing sedimentary nutrients back into the water column (Golterman et al. 1969; McCarter et al. 1952; Mortimer 1941; Lee et al. 1977). Lam and Jaquet (1976) showed that after periods of high wind on the Great Lakes, phosphorus concentrations were elevated. Ryding and Forsberg (1977) showed a correlation between water quality and orientation of the long axis of Lake Uttran in Sweden to the prevailing winds "... indicating that mixing plays a dominant role for the transport of nutrients from the sediments in shallow lakes." The effects of resuspension on shallow eutrophic lakes, or indeed the actual occurrence of resuspension, however, have not been quantitatively measured.

Engineers working with problems of beach erosion have developed a number of quantitative models of wave action based on oceanographic theory and empirical observations (U.S. Army Coastal Engineering Research Center 1977). In this paper we apply these ideas to a prairie lake to determine when we might expect to find wind resuspension of bottom sediments. Our objectives were to determine if existing theory can be used to predict when sediment resuspension will occur, and to develop a quantitative method for expressing how often and to what extent sediment resuspension might occur in shallow lakes.

[1]Journal paper No. J-11187 of the Iowa Agriculture and Home Economics Experiment Station, Ames, IA. Project 2483.

Theory

Surface waves are produced when wind blows across a lake. Although the resulting water motion is often very complex, simple mathematical theories for ideal waves can usually be used to predict many aspects of the behavior of real waves. If waves are traveling in water with a depth greater than one-half of their wavelengths, they are called deepwater waves. The water particles at the surface follow approximately circular paths as each wave passes by. The radius of the circle is equal to one-half the wave height for particles at the surface and decreases exponentially with depth. When a deepwater wave moves into water with a depth less than one-half its wavelength, the wave is said to "feel" the bottom. The orbits of the water particles become elliptical rather than circular, and there is an oscillatory horizontal motion of the water immediately over the bottom sediments which may be sufficient to resuspend bottom sediments.

The wavelength of a deepwater wave is related to its period by the equation

$$(1)\quad L = \frac{gT^2}{2\pi}$$

where L is the wavelength (metres), g is the gravitational constant ($9.8\ \mathrm{m \cdot s^{-1} \cdot s^{-1}}$), and T the wave period (seconds). The period of wind-driven waves is determined by wind velocity, wind fetch (distance over water that the wind blows), and wind

duration. In small lakes we may simplify this by assuming that the wind has a constant velocity over a period of say 1 h. Wave period is related to wind velocity and fetch by the following empirical equation (U.S. Army Coastal Engineering Research Center 1977):

$$(2)\quad \frac{gT}{2\pi U} = 1.20 \tanh\left[0.077\left(\frac{gF}{U^2}\right)^{0.25}\right]$$

where U is the wind velocity (metres per second) and F is the effective fetch (metres). Thus, if we know the wind velocity and fetch on a lake, we can calculate the resulting wave period with Equation 2 and use that value in Equation 1 to calculate the wavelength. We can then determine if the wave base (assumed to be one-half the wavelength) extends to the lake bottom at any given location.

Methods

Little Wall Lake, Iowa (42°16′N, 93°38′W) is a shallow unstratified prairie lake with a mean depth of 1.3 m and a maximum depth of 1.7 m (Fig. 1). It has a surface area of 104 ha and is surrounded by open, gently rolling topography. A lake survey in 1979 showed that the lake was highly eutrophic with summer levels of chlorophyll *a* of 50 mg·m^{-3}, total phosphorus of 172 mg·m^{-3}, total nitrogen of 2.2 mg·L^{-1}, and Secchi disk depth of 1.0 m.

To measure wind resuspension of bottom sediments, we used a system of pumps and hoses to pump lake water from two sites (Fig. 1). Site 1 was located at the north end of the lake, approximately 100 m offshore, and site 2 was located off of the east shore of the lake. Depth at site 1 was 1.2 m, and site 2 had a depth of 1.5 m. Both sites were exposed to the southerly winds that predominate in the summer. Water samples were collected during the summer and fall of 1982 from three depths by using an arrangement consisting of a float at the water surface anchored to two cement blocks on the lake bottom. Three polyethylene tubes (6.3-mm diameter) ran from the buoy system to the shore. Sampling depths at site 1 were 0.3, 0.6, and 0.9 m, and depths at site 2 were 0.37, 0.75, and 1.12 m. On shore, the three tubes ended in a manifold and a pump. By opening and shutting valves, it was possible to sample the three depths independently or simultaneously.

A comparison of samples collected by use of the pumps with samples taken in the lake at the same times with a Van Dorn water sampler on eight different occasions (Carper 1983) showed that there were small differences in the values for some particulate variables at site 1. There were strong statistical correlations (r values from 0.85 to 0.97) for measurements of the particulate variables made on samples taken from the lake with a water bottle and those taken with the pump. Thus, we concluded that the pump samples could be used as an indication of changes in the values of particulate variables in the lake even though the absolute values may be imprecise. Sediment samples were collected at sites 1, 2, and 3 (Fig. 1), and these were analyzed for particle size distribution and organic matter content.

Biweekly sampling times were established to provide background information against which changes caused by major wind events could be compared. Increased sampling occurred during high wind periods and the period immediately following such events. Sampling occurred in 41 days. Wind velocity was recorded continuously at one location on the lake by using a cup anemometer linked with a recorder. Wind direction was noted at

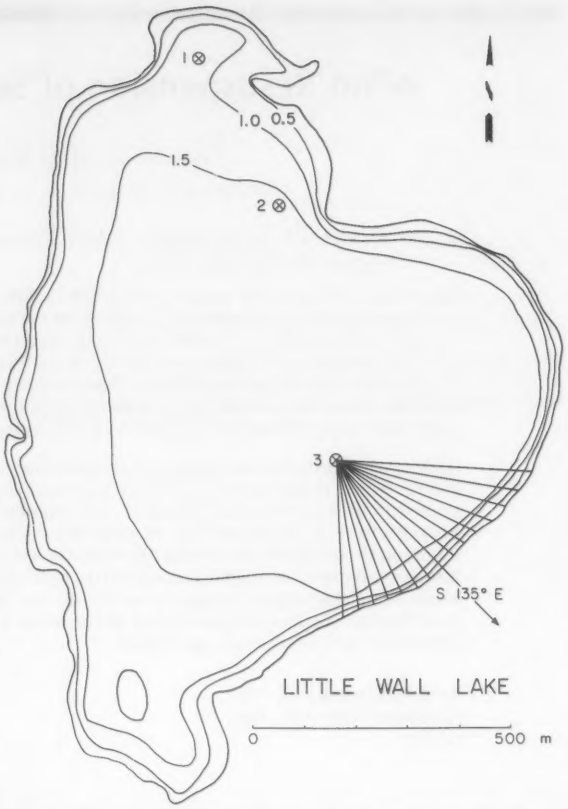

FIG. 1. Location of sampling sites in Little Wall Lake. Site 3 was used only for sediment sampling. Radial lines used for calculating the effective fetch for winds from the southeast are shown for site 3.

sampling times. To fill in gaps in the wind record resulting from equipment failures, additional wind data were obtained from a weather station at Ames, Iowa, approximately 32 km from Little Wall Lake. A regression equation based on paired readings at both sites was used to estimate the missing values.

Fetch lengths were calculated for sites 1 and 2. In lakes where fetches are limited by landforms surrounding the water body, the fetch length is often long relative to the fetch width. This reduces the effective fetch and results in smaller waves than would be produced from the same winds in the open ocean. This is corrected for by calculating an effective fetch (U.S. Army Coastal Engineering Research Center 1977). The procedure is to plot the station position on a lake map and draw a line from the station to the shore in the direction from which the wind is blowing (Fig. 1). Other radial lines are drawn from the station to the shore at intervals of 6° so that there are seven lines on each side (the seventh line on each side will be at an angle of 42° from the center line). The length of each radial is multiplied times the square of the cosine of the angle between the radial and the wind direction. These values are summed and divided by the sum of the cosines of all the angles (13.5) to yield the effective fetch length. Once the fetch is known, Equation 2 can be used to calculate the period for any wind velocity, and Equation 1 can be used to calculate the wavelength. Wave base is assumed to be one-half the wavelength.

Water samples were analyzed for total filtrable and total

nonfiltrable phosphorus, total, organic, and inorganic suspended solids, chlorophyll *a*, turbidity, conductivity, and pH. Phosphorus was analyzed according to the procedures of Murphy and Riley (1962) with a persulfate oxidation (Menzel and Corwin 1965). Total filtrable phosphorus was analyzed in the same way with the addition of a filtration step (American Public Health Association 1975). Chlorophyll *a* samples were extracted according to the methods of Yentsch and Menzel (1963) with the exception that 90% acetone was used instead of 85% acetone. Chlorophyll *a* was determined according to the equations of Parsons and Strickland (1963), total suspended solids according to standard methods (American Public Health Association 1975), turbidity with a Hach turbidimeter (model 2100), specific conductance by using a Hach conductivity meter (model 2511), and pH with an Orion Research ionanalyzer (model 407A).

To calculate the extent that winds from a given direction will disturb the lake bottom, we located a network of stations on a bathymetric map of the lake and calculated the effective fetch for that wind for each station. These values were plotted on the map, and contour lines of equal fetch length (100, 200, 300 m, etc.) were plotted. For each fetch line, mixing depths (one-half the wavelength) were calculated for wind velocities from 5 to 60 $km \cdot h^{-1}$ in increments of 5 $km \cdot h^{-1}$. For example, for a fetch of 200 m and a wind velocity of 30 $km \cdot h^{-1}$, the wavelength will be such that the wave action will extend down to a depth of 0.99 m. Those locations where the 200-m fetch line intersects the 1-m contour line will be on a line dividing those parts of the lake where the waves extend to the bottom from those where they do not. For each fetch, these points were found, and contour lines for each velocity were drawn on the map. A planimeter was then used to determine the percentage of the lake area influenced by each wind velocity.

To determine the frequency of wind mixing, it was necessary to know something about the character of the wind in the area. We analyzed 5 yr of wind data from the Des Moines, Iowa, airport (U.S. Department of Commerce 1982). Wind velocities and directions at the airport are recorded every 3 h. We tabulated all the 3-h readings for the months of June, July, and August for the 5-yr period 1978–82. We sorted the observations into four wind directions (northeast, southeast, southwest, northwest). The wind came from the southeast most frequently (40% of the time), with the southwest (20%) being next, followed by northwest (17%) and northeast (17%) winds. There were no measureable winds reported 5% of the time. We tabulated the frequencies of the various wind velocities from the southeast and combined these with the relationship between wind velocity and area of the lake bed subject to waves. This yielded a frequency distribution of the percentage of the time that winds from the southeast will influence various areas of the lake.

Results and Discussion

From 14 to 21% of the dry weight of the sediment samples was organic matter. The high inorganic content of the sediments contrasts with the high organic content of the suspended materials found on most days (Table 1) and provides a means of identifying resuspended sediments. Particle size distributions were similar for the three sites, with a median size of about 0.05 mm and almost no particles over 2 mm in diameter. This indicates that most of the sediment is in the silt and clay size range and should be subject to resuspension.

We found no significant differences in the values of the characteristics measured at the different depths (Table 1), indicating a well-mixed lake. Therefore, we averaged the values for the variables over depth, so that there was only one value for each variable for each site for each sampling time. These are the data upon which all further analyses were based.

TABLE 1. Comparisons of mean values of measured characteristics over three sampling depths. Observations for sites 1 and 2 are combined.

	Position in water column		
	Top	Middle	Bottom
Chlorophyll *a* ($mg \cdot m^{-3}$)	93.7	90.4	84.2
Phaeophytin ($mg \cdot m^{-3}$)	22.3	20.67	21.4
Total susp. solids ($mg \cdot L^{-1}$)	16.47	15.07	14.86
Inorganic susp. solids ($mg \cdot L^{-1}$)	2.96	2.27	2.66
Organic susp. solids ($mg \cdot L^{-1}$)	13.5	12.8	12.2
Total phosphorus ($mg \cdot L^{-1}$)	0.161	0.158	0.157
Filtrable phosphorus ($mg \cdot L^{-1}$)	0.078	0.076	0.078
Particulate phosphorus ($mg \cdot L^{-1}$)	0.083	0.082	0.079
Specific conductance ($\mu S \cdot cm^{-1}$)	418	416	419
pH	8.9	8.9	8.9
Turbidity (NTU)	11.6	11.4	10.7

Southeasterly winds predominated on our sampling days. The wind blew out of the southeast on 19 days, the northwest on 9 days, the northeast on 8 days, and the southwest on 5 days. Effective fetches were calculated for winds from the southeast (135°) for sites 1 and 2. At site 1 the effective fetch is 670 m and the water depth is 1.2 m. For site 2 the fetch is also 670 m and the depth is 1.5 m. Wind velocities required to produce waves with a base reaching the lake bottom calculated from Equations 1 and 2 are 20.5 $km \cdot h^{-1}$ for site 1 and 25.5 $km \cdot h^{-1}$ for site 2.

High densities of plankton algae in the lake and associated high levels of total phosphorus, chlorophyll *a*, and turbidity (Table 1) masked increases that might have occurred by wind resuspension. This, however, was not true for inorganic suspended solids. At site 1 there were 4 d on which the wind velocity exceeded the critical velocity (Fig. 2). On each of these days the inorganic suspended solids values were all larger than any other value of inorganic suspended solids measured during the study at this site. For site 2 there was only 1 d on which the critical velocity was exceeded. Again, the measurement of inorganic suspended solids was much larger than any other value for the sampling period. Since the bottom sediments are high in inorganic material, this is direct evidence for sediment resuspension when winds exceed the critical velocity.

Since our field measurements support our hypothesis that sediments are resuspended when the calculated wavelengths exceeded twice the water depth, we proceeded to calculate the areas of this lake subject to sediment resuspension at various wind velocities (Fig. 3). Note that there is relatively little effect until a wind velocity of about 15 $km \cdot h^{-1}$ is reached. Above that velocity there is an increasing effect of wind mixing. When this distribution is combined with the wind frequencies from the southeast, we found that most of the time only a small portion of the lake sediments are subject to wave action (Fig. 4). Wave base reaches 50% of the lake bed less than 1% of the time.

Hakanson (1981) recognized three regions of lake sediments: areas of erosion, transportation, and accumulation. Areas of erosion are found where wave action prevents the deposition of fine sediments. These are the areas shown at the right of Fig. 4 that are disturbed by the most frequent wind velocities. Few sediments are available for resuspension from this area. Areas

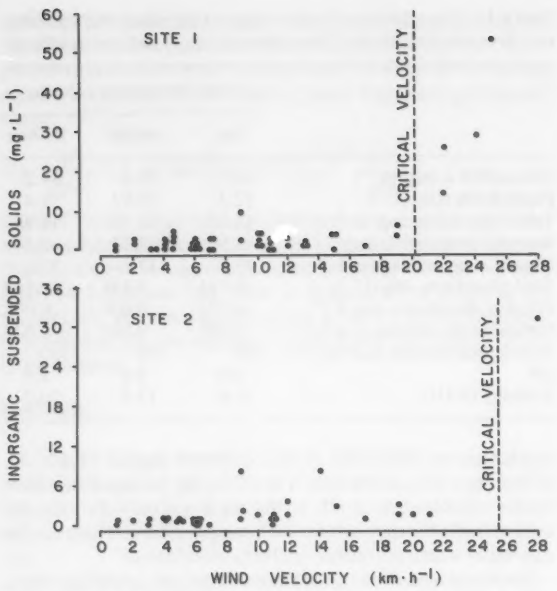

FIG. 2. Plots of inorganic suspended solids vs. wind velocity at sampling time.

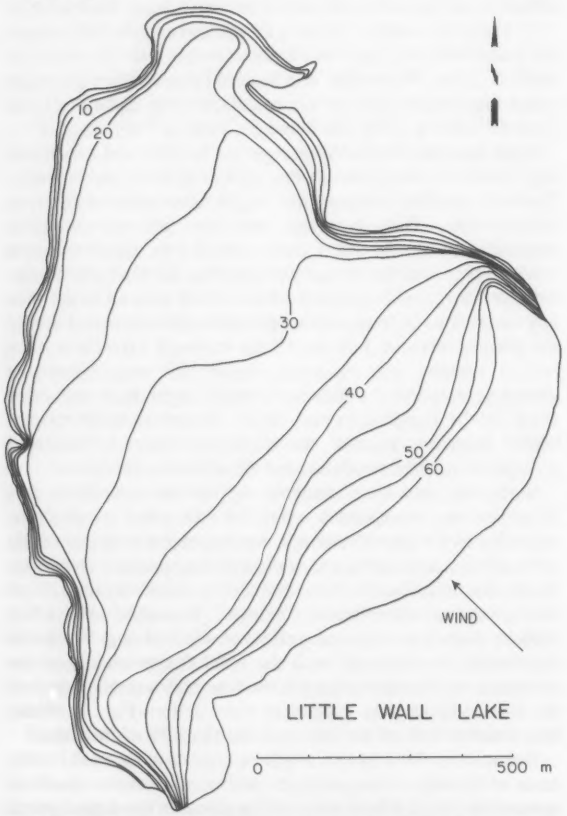

FIG. 3. Contours showing the wind velocities ($km \cdot h^{-1}$) necessary for resuspension to occur for a southeasterly wind. The areas northwest of the contours will be mixed to the bottom at the indicated velocities.

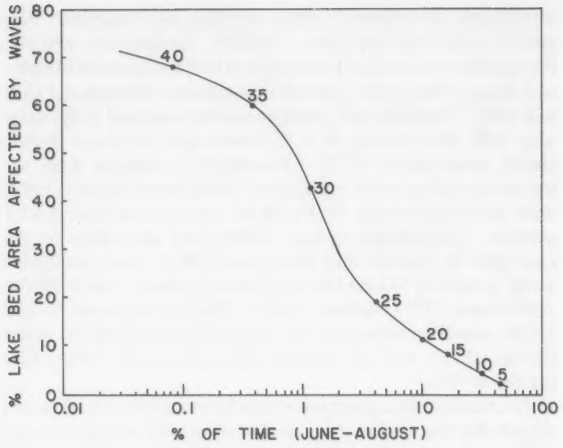

FIG. 4. Percentage of the lake bed affected by winds from the southeast vs. the frequency of occurrence of those winds in June through August. The numbers above the curve are corresponding wind speeds ($km \cdot h^{-1}$).

of transportation are characterized by the discontinuous deposition of fine sediments. Fine sediments deposited in these areas during average wind conditions are resuspended by the infrequent strong winds indicated by the middle and left portions of Fig. 4. This will be the source of most resuspended sediments. Fine particles are deposited continuously in the areas of accumulation. Here the sediments are beyond the reach of the effects of surface waves. The extent of this region is shown by the portions above the curve at the far left in Fig. 4. No resuspension will occur in this area of the sediments.

The field measurements in this study showed that when water depths were less than one-half the calculated wavelength for surface waves, sediment resuspension occurred in Little Wall Lake. The same is likely to be true of other lakes with similar sediment characteristics. The map we developed to show the areas of the lake affected by winds of different velocities (Fig. 3) is a useful method of indicating where in a lake sediment resuspension is most likely to occur. The curve (Fig. 4) showing the probabilities that different percentages of the lake bed will be affected by waves driven by the prevailing wind summarizes information on both the lake morphometry and local wind distribution. We suggest that this curve is a useful, descriptive tool for comparing lakes and may also have direct application in predicting water quality in new lakes or in determining the effects of lake deepening projects.

Acknowledgments

We thank Daniel Canfield Jr. for sharing his preliminary work on the lake sampling device and for providing editorial assistance. Kenneth Kortge and Thomas Robertson assisted in field work and laboratory analyses. Dr. C. H. Mortimer provided valuable suggestions for improvement of the manuscript.

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Effects of Perfusate HCO_3^- and P_{CO_2} on Chloride Uptake in Perfused Gills of Rainbow Trout (*Salmo gairdneri*)

S. F. Perry,[1] P. Payan, and J. P. Girard

Laboratoire de Physiologie Comparée, Faculté des Sciences, Université de Nice, Parc Valrose, 06034 Nice Cedex France

Perry, S. F., P. Payan, and J. P. Girard. 1984. Effects of perfusate HCO_3^- and P_{CO_2} on chloride uptake in perfused gills of rainbow trout (*Salmo gairdneri*). Can. J. Fish. Aquat. Sci. 41: 1768–1773.

Experiments were conducted using a saline-perfused trout (*Salmo gairdneri*) head preparation in an attempt to determine the origin of HCO_3^- involved in gill apical Cl^-/HCO_3^- exchange, the possibilities being plasma CO_2 or HCO_3^-. Initial results showed that branchial Cl^- influx was stimulated both by increased perfusate $[HCO_3^-]$ and P_{CO_2}. Subsequent experiments employing the chloride transport inhibitors, SITS and thiocyanate, indicated that stimulation of Cl^- influx by HCO_3^- probably was due to gill hemodynamic alterations and not to increased entry of HCO_3^- into the gill epithelium. We conclude that CO_2 entry into the gill epithelium from plasma and its subsequent hydration to HCO_3^- and H^+, by carbonic anhydrase, is a major pathway by which HCO_3^- for Cl^-/HCO_3^- exchange is generated.

Nous avons réalisé des expériences sur une préparation de tête de truite (*Salmo gairdneri*) soumise à une perfusion de solution saline afin de connaître l'origine du HCO_3^- mis en jeu dans l'échange de Cl^- et de HCO_3^- qui se produit dans la région apicale des branchies, les possibilités à considérer étant le CO_2 et le HCO_3^- plasmatiques. Les premiers résultats ont indiqué que l'élévation de la concentration de HCO_3^- ou de P_{CO_2} dans le liquide de perfusion stimule l'afflux branchial de Cl^-. Nous avons réalisé d'autres expériences avec des inhibiteurs du mouvement du chlorure, soit SITS et le thiocyanate ; nous avons constaté que l'action stimulante du HCO_3^- sur l'afflux de Cl^- est probablement due à un changement de l'hémodynamique dans les branchies, non à l'augmentation de la quantité de HCO_3^- pénétrant dans l'épithélium. Nous en concluons que la pénétration du CO_2 plasmatique dans l'épithélium des branchies et sa transformation en HCO_3^- et H^- sous l'action de l'anhydrase carbonique représente l'une des principales voies de production de HCO_3^- pour l'échange de HCO_3^- et de Cl^-.

Received March 27, 1984
Accepted August 31, 1984
(J7740)

Reçu le 27 mars 1984
Accepté le 31 août 1984

In recent years various studies have been conducted to examine two conflicting theories of carbon dioxide excretion in fish. As a result, it is now generally accepted that the involvement of fish erythrocytes in CO_2 elimination is similar to that which has been shown for mammals (Cameron 1978; Obaid et al. 1979; Perry et al. 1982; Wood et al. 1982; Heming and Randall 1982). These investigations have aided in disproving the hypothesis of Haswell et al. (1980) that the fish erythrocyte is functionally impermeable to plasma HCO_3^-; they proposed a model in which the entry of plasma HCO_3^- into gill epithelial cells is the rate-limiting step in CO_2 excretion and a source of HCO_3^- for gill apical Cl^-/HCO_3^- exchange. This view opposes the classic model of Maetz and co-workers in which the origin of HCO_3^- for gill Cl^-/HCO_3^- exchange is intra-branchial hydration of plasma CO_2, catalyzed by carbonic anhydrase (see Maetz 1971, 1974). While it now appears that direct entry of plasma HCO_3^- into the branchial epithelium is not involved in CO_2 excretion in fish (Perry et al. 1982), its involvement in Cl^-/HCO_3^- exchange is less clear.

In this study we used an isolated saline-perfused head preparation to determine the pattern of CO_2 movement across the gill epithelium of rainbow trout (*Salmo gairdneri*). More precisely, we attempted to determine whether the HCO_3^- exchanged for Cl^- at the apical surface of the gill epithelium arises directly from plasma HCO_3^- or from the hydration of plasma CO_2. If HCO_3^- involved in apical Cl^-/HCO_3^- exchange originates from hydration of plasma CO_2 within gill epithelial cells, we would expect only perfusate P_{CO_2} to affect Cl^- influx. Alternatively, if HCO_3^- for apical Cl^-/HCO_3^- exchange arises from the direct movement of plasma HCO_3^- into the gill epithelium, we would expect only perfusate HCO_3^- concentration to affect Cl^- influx.

Materials and Methods

Rainbow trout of either sex, weighing between 150 and 200 g, were obtained from a fish hatchery near the University of Nice. They were maintained in polyethylene holding tanks in a temperature controlled room and supplied with dechlorinated tap water ($[Na^+] = 0.1$ mmol/L, $[Cl^-] = 0.07$ mmol/L, $[Ca^{2+}] = 1.3$ mmol/L, temperature = 16°C) for periods never exceeding 3 wk. Fish were not fed during the holding period.

Isolated, saline-perfused head preparations were prepared according to the method of Payan and Matty (1975) with slight modifications. Fish were injected intraperitoneally with sodium heparin (2500 USP units/fish). After 20 min, the fish was decapitated just caudad of the pectoral fins, the head was placed onto an operating table, and the gills were irrigated with freshwater via a tube placed into the mouth. Immediately, the

[1]Present address: Department of Biology, University of Ottawa, 30 Somerset E., Ottawa, Ont. K1N 6N5.

pericardium was cut and the ventricle severed to prevent air from being pumped into the gill vasculature. Viscera were removed from the body cavity, and a catheter was inserted into the bulbus arteriosus through the severed ventricle and tied in place. The gills were cleared of blood while the head was on the operating table by perfusing with filtered (Millipore, 0.22 μm) air-equilibrated saline (Payan and Matty 1975; modified according to Perry et al. 1984c) at a constant pressure of 4.9 kPa (50 cmH_2O). A tightly fitting semicircular plastic collar was placed inside the abdominal cavity, thus making the body wall rigid. Finally, a catheter was inserted into the dorsal aorta for collection of post-branchial saline. The surgery was completed in approximately 8 min. At this time, the gills were inspected visually to determine effectiveness of red blood cell (RBC) clearance. Heads that displayed inadequate gill RBC clearance (less than 90% by visual inspection) were discarded.

The head was removed from the operating table, placed into a cylindrical plastic container, and held in place by a thin rubber membrane (balloon or condom) which prevented leakage of the recirculating solution contained inside. The head was irrigated at approximately 500 mL/min with a 1 mmol/L NaCl solution (in tap water) by a tube placed into the mouth. Temperature of the external medium was maintained at 16°C by recirculation through coils immersed in a cooling bath. The gills were perfused at constant pulsatile flow (4.5 mL/min) from a double reservoir, with gas-equilibrated saline (0.3% CO_2 in air or 1% CO_2 in air during high P_{CO_2} experiments) using a cardiac pump. Gas mixtures were supplied by gas mixing pumps (Godart). Dorsal aortic pressure was kept at zero in all experiments. Input pressure was monitored via a T-junction in the input catheter connected to a Statham P23dB pressure transducer and displayed on a chart recorder. Isolated heads that exhibited input pressure greater than 5.9 kPa (60 cmH_2O) usually were indicative of trapped air bubbles in the branchial vasculature, and were discarded. Heads were perfused for 5–10 min (or until input pressure had stabilized) using the appropriate perfusate conditions (e.g. low $[HCO_3^-]$, 0.3% CO_2; 13 mmol/L $[HCO_3^-]$, 1.0% CO_2; etc.) before experiments were begun. All experiments were performed using 10^{-6} mol/L norepinephrine (Arterenol; Sigma) in the perfusate in order to stimulate Cl^- influx (Perry et al. 1984c).

Experiments consisted of monitoring Cl^- influx (J_iCl^-), external Cl^- concentration, and input pressure (P_{in}) while adjusting perfusate P_{CO_2} and $[HCO_3^-]$ or adding the drugs 4-acetamido-4′-iso-thiocyanatostilbene-2,2′-disulfonic acid (SITS, 10^{-3} mol/L; British Drug House) and sodium thiocyanate (10^{-3} mol/L) to the perfusate and water, respectively. Changing from one experimental condition to another was accomplished by switching saline reservoirs by means of a three-way tap, with no interruption in flow. $[HCO_3^-]$ was adjusted by adding known amounts of $NaHCO_3$, while P_{CO_2} was altered by adjusting the gas mixing pumps.

pH measurements were made with a Radiometer PHM-72 digital acid–base analyser and associated micro pH electrode (G297/G2 capillary electrode) at 16°C. Total carbon dioxide (C_{CO2}) was determined using a CO_2 analyser (Corning model 905). Partial pressures of carbon dioxide (P_{CO_2}) and bicarbonate concentrations were calculated using the measured pH and C_{CO2} values and a reorganization of the Henderson–Hasselbalch equation as follows:

$$(1)\quad P_{CO_2} = \frac{C_{CO2}}{\text{antilog}\,(\text{pH} - \text{pK}')\alpha CO_2 + \alpha CO_2}$$

$$(2)\quad [HCO_3^-] = C_{CO2} - (\alpha CO_2)(P_{CO_2}).$$

The operational pK′ values of carbonic acid were obtained from Severinghaus et al. (1956), and the solubility coefficient of CO_2 (αCO_2) was obtained from Albers (1970).

J_iCl^- was determined by following the specific activity of the external medium (CPM ext./Cl^- ext.) and the appearance of $^{36}Cl^-$ radioactivity in the dorsal aorta (see equation 3). The contribution of the arterial–venous (A–V) pathway to Cl^- uptake was not investigated because results of previous studies have shown the A–V pathway to be unimportant for ionic uptake in freshwater salmonids (Girard and Payan 1980). Approximately 0.01 MBq (0.3 μCi) of $^{36}Cl^-$ (as NaCl) was added to the external medium (volume = 150 mL), and following 5 min of mixing, simultaneous samples were taken from the external medium and dorsal aorta every 5 min for the duration of the experiment. $^{36}Cl^-$ activity was determined using liquid scintillation counting. Correction for quenching was not necessary, as all samples showed identical counting efficiency. External Cl^- concentration was determined using a Technicon autoanalyser. J_iCl^- (micromoles per 100 g per hour) was calculated using the following equation:

$$(3)\quad J_iCl^- = \frac{\text{CPM}/\mu\text{L DA}\cdot\dot{Q}(\mu\text{L/min})\cdot 60\cdot 100/\text{fish weight (g)}}{\text{Specific activity external medium (CPM}/\mu\text{mol)}}$$

where DA = dorsal aorta and $\dot{Q}$ = perfusion flow rate.

Upon termination of each experiment, the gills were examined visually once again, and in all cases RBC clearance appeared to be 100%. The gills were not examined microscopically, but a recent study (Perry et al. 1984b) has shown that gills perfused for 30 min under similar conditions exhibited no edema formation or other structural abnormalities.

In the illustrations, time zero represents the beginning of an experiment following a 5- to 10-min stabilization period. Variability of the data is indicated by ±1 SE. Results were statistically analysed by comparing sample means using Student's paired two-tailed t-test, and 5% was taken as the fiducial limit of confidence.

Results

At constant P_{CO_2}, increasing the concentration of $NaHCO_3^-$ from approximately zero (0.4 mmol/L) to 5 mmol/L or from approximately zero to 13 mmol/L resulted in significant 50 and 85% increases in Cl^- influx, respectively (Fig. 1). Raising $[HCO_3^-]$ from 13 to 26 mmol/L caused a significant reduction in J_iCl^-. Similar stimulation of J_iCl^- by $NaHCO_3^-$ also was observed (112% stimulation) following addition of 10^{-3} mol/L SITS (an anion transport inhibitor) to the perfusate (Fig. 2). Adding 10^{-3} mol/L sodium thiocyanate (a chloride transport inhibitor) to the external medium also did not abolish the stimulatory effect of $NaHCO_3^-$ on J_iCl^- (200% stimulation) although it did inhibit J_iCl^- in low HCO_3^- saline (0.4 mmol/L) as indicated by decreasing J_iCl^- prior to $NaHCO_3^-$ addition (Fig. 2). The substantial difference in J_iCl^- between the two groups perfused with low HCO_3^- saline (Fig. 1) is difficult to explain but probably reflects large variability among the various treatment groups. For this reason, we have made no attempt to statistically analyse differences between the treatment groups but have compared differences only within each particular group.

Under conditions of constant P_{CO_2}, the addition of $NaHCO_3^-$ to low HCO_3^- saline caused a large increase in pH (Table 1) and

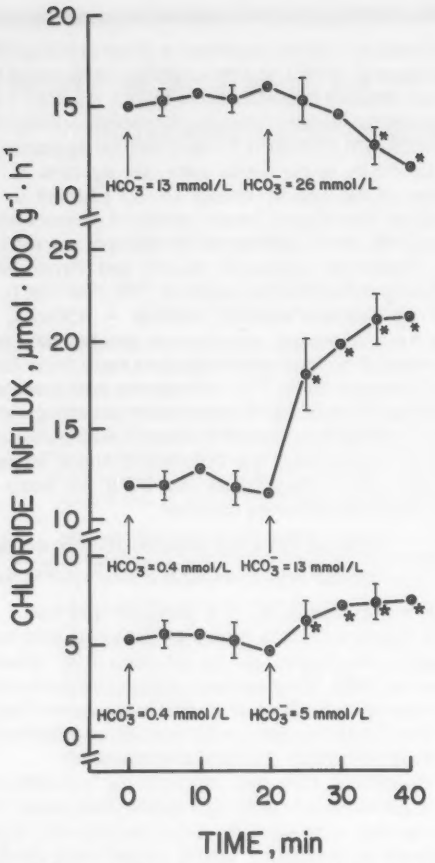

FIG. 1. Effect of perfusate $[HCO_3^-]$ on Cl^- influx in the isolated, saline-perfused head of rainbow trout ($n = 4$ different fish for each treatment). Statistical treatment: paired data comparison between each experimental value and final value of preceding treatment taken as reference. Asterisk indicates $p \leq 0.05$.

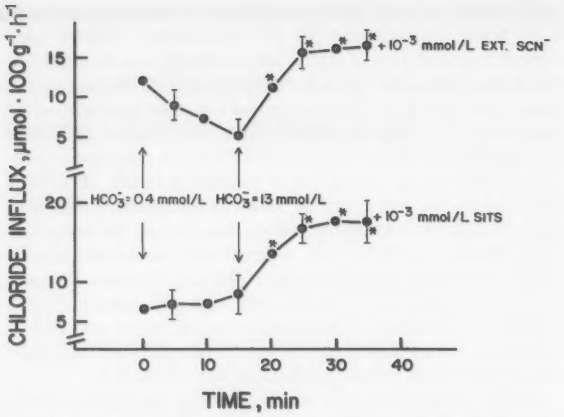

FIG. 2. Effect of perfusate $[HCO_3^-]$ on Cl^- influx in the isolated, saline-perfused head of rainbow trout following addition of either 10^{-3} mol/L SITS ($n = 4$) to the perfusate or 10^{-3} mol/L thiocyanate ($n = 4$) to the external medium. Statistical treatment: paired data comparison between each experimental value and final value of preceding treatment taken as reference. Asterisk indicates $p \leq 0.05$.

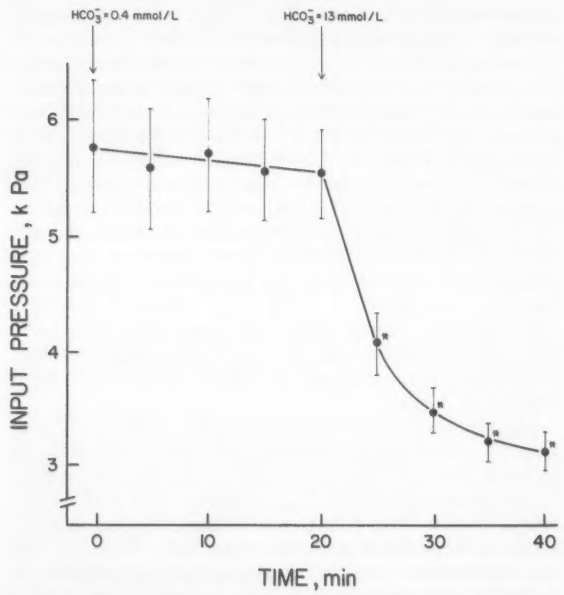

FIG. 3. Effect of perfusate $[HCO_3^-]$ on input pressure in the isolated, saline-perfused head of rainbow trout ($n = 5$). Statistical treatment: paired data comparison between each experimental value and final value of preceding treatment taken as reference. Asterisk indicates $p \leq 0.05$.

was associated with a large decrease in input pressure (Fig. 3). Changing to 5 mmol/L HCO_3^- saline caused a lesser increase in pH (Table 1) and was associated with a smaller reduction of input pressure. Switching from 13 to 26 mmol/L HCO_3^- saline, however, was without effect on input pressure although once again pH was increased (8.0–8.3).

Changing from saline gassed with 1% CO_2 (P_{CO_2} = 1027 Pa = 7.7 Torr, Table 1) to saline gassed only with air (P_{CO_2} = 187 Pa = 1.4 Torr, Table 1) caused a large reduction in $J_i Cl^-$ which was partially restored to initial levels by switching back to 1% CO_2 (Fig. 4). In contrast with the previous experiments, adjustments of $J_i Cl^-$ did not significantly affect input pressure, although once again there was a large change in perfusate pH (Table 1). Due to the low buffering capacity of the perfusate (−2.62 Slykes, L. Milligan, McMaster University, Hamilton, Ont., pers. comm.) changes in saline $[HCO_3^-]$ were minimal as P_{CO_2} was adjusted (Table 1).

Discussion

The isolated, saline-perfused head preparation was selected for the present investigation because it meets several of the criteria of a successful perfused preparation: the surgical preparation is rapid, long periods of branchial ischemia are avoided, the gills are well-irrigated and perfused, the volume of the external medium is small (approximately 150 mL depending on size of the head), and most importantly, the preparation does not leak (i.e. $Q_{in} = Q_{out}$; see review by Perry et al. 1984a). Although the perfused trout head preparation suffers from various limitations, including lack of dorsal aortic pressure, it is apparent that Cl^- uptake was stable and similar to in vivo values

TABLE 1. Measured (C_{CO2} and pH) and calculated ([HCO_3^-] and P_{CO_2}) acid–base variables of perfusate during manipulations of P_{CO_2} and [HCO_3^-].

	Perfusate condition					
	Low HCO_3^-	5 mmol/L HCO_3^-	13 mmol/L HCO_3^-	26 mmol/L HCO_3^-	Low P_{CO_2}	1% CO_2
C_{CO2} (mmol/L)	0.6	5.0	13.0	26.1	12.9	15.5
[HCO_3^-] (mmol/L)	0.4	4.8	12.9	25.9	12.8	13.9
P_{CO_2} (Torr)	2.7	2.8	2.6	2.9	1.4	7.7
(Pa)	360	393	347	387	187	1027
pH	6.92	7.65	8.04	8.30	8.22	7.61

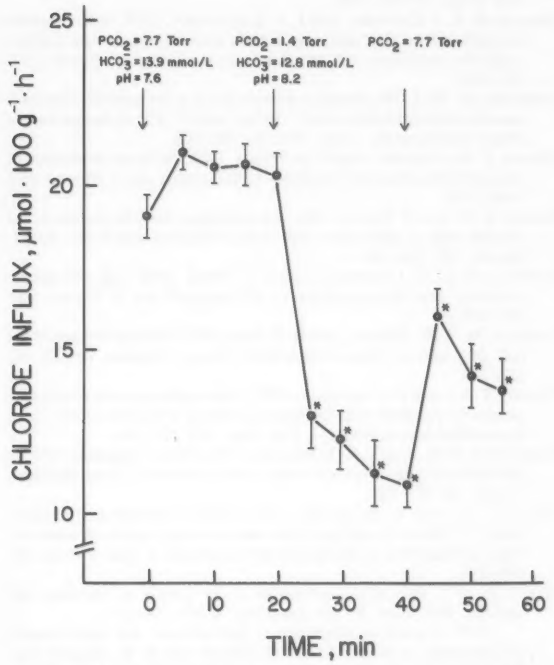

FIG. 4. Effect of perfusate P_{CO_2} (7.7 Torr = 1027 Pa; 1.4 Torr = 187 Pa) on Cl^- influx in the isolated, saline-perfused head of rainbow trout ($n = 3$). Statistical treatment: paired data comparison between each experimental value and final value of preceding treatment taken as reference. Asterisk indicates $p \leq 0.05$.

(~150 mmol·kg^{-1}·h^{-1}; McDonald et al. 1983) during our experiments.

These experiments were not performed in vivo because of the inability to specifically alter the chemical or gas composition of the blood entering the gills. Moreover, the objective of this study was to assess the movement of CO_2 across only the gill epithelium. Clearly, the presence of red blood cells would complicate the analysis. For this reason, isolated heads were perfused with saline and not blood.

Our results show that branchial Cl^- influx is directly related to the concentration of $NaHCO_3^-$ in the perfusate within the range of 0–13 mmol/L, and at first glance support the theory that HCO_3^- entry from plasma into the gill epithelium occurs and is an important step in apical Cl^-/HCO_3^- exchange. However, there are reasons to believe that the stimulatory effect of $NaHCO_3^-$ on J_iCl^- may be secondary in nature. The disulfonic stilbene derivative, SITS, inhibits anion movements (HCO_3^- and Cl^-) in gill epithelial cells when applied externally (Perry and Randall 1981), in opercular epithelium (Degnan et al. 1977), red blood cells (Knauf and Rothstein 1971; Cabantchik and Rothstein 1972; Haswell et al. 1978; Shami et al. 1978; Cabantchik et al. 1978), turtle bladder (Cohen et al. 1978), squid axon (Russell and Boron 1976), and *Aplysia* neurones (Russell 1978). The fact that SITS, when applied internally, had no effect on Cl^- influx stimulated by HCO_3^- is surprising given the previous information. One must either assume that SITS is ineffective in blocking HCO_3^- entry into the gill epithelium or that this process does not take place to any large extent. The latter choice is more likely, especially considering the high concentration of SITS (10^{-3} mol/L) used (lower concentrations were equally ineffective in blocking Cl^- uptake).

Furthermore, thiocyanate, a potent inhibitor of branchial Cl^-/HCO_3^- exchange in fish (Epstein et al. 1973; Kerstetter and Kirschner 1974; de Renzis 1975), also was without effect on Cl^- influx stimulated by HCO_3^- although it did inhibit J_iCl^- during perfusion with low HCO_3^- saline; only in this group did J_iCl^- decline significantly during the period preceding the change in $NaHCO_3^-$. Given these results, how does one explain the stimulatory effect of $NaHCO_3^-$ on Cl^- uptake? A possible explanation is the large reduction of input pressure associated with $NaHCO_3^-$ addition, indicating substantial branchial vasodilation. Thus, it is possible that Cl^- influx is enhanced simply by an increase in gill functional surface area, considering that a decrease in input pressure normally reflects a greater surface area perfused. Depending on the concentration of $NaHCO_3^-$ used, perfused preparations displayed varying degrees of input pressure reduction; SITS and thiocyanate were without effect on input pressure. It is apparent that J_iCl^- is stimulated to the greatest extent when input pressure is reduced to the greatest extent (Fig. 5). Interestingly, changing the concentration of perfusate $NaHCO_3^-$ from 13 to 26 mmol/L caused no change in input pressure, and Cl^- uptake was not stimulated. This would indicate that the hemodynamic effect of $NaHCO_3^-$ is maximal at 13 mmol/L. An alternate explanation for the stimulatory effect of $NaHCO_3^-$ on J_iCl^- is a direct pH effect, since perfusate pH varied considerably as $NaHCO_3^-$ levels were altered at constant P_{CO_2} (Table 1). This seems unlikely, however, since stimulation of Cl^- uptake following $NaHCO_3^-$ addition was associated with an elevated perfusate pH whereas stimulation of J_iCl^- by increasing P_{CO_2} was associated with decreased pH. It is difficult to imagine similar changes in J_iCl^- being caused by opposite changes in perfusate pH. It seems more likely that H^+ exerts an effect on J_iCl^- indirectly via hemodynamic alterations. The hemodynamic changes were prevalent only when pH was raised from values well outside of the normal physiological range (i.e. "low" [HCO_3^-] to

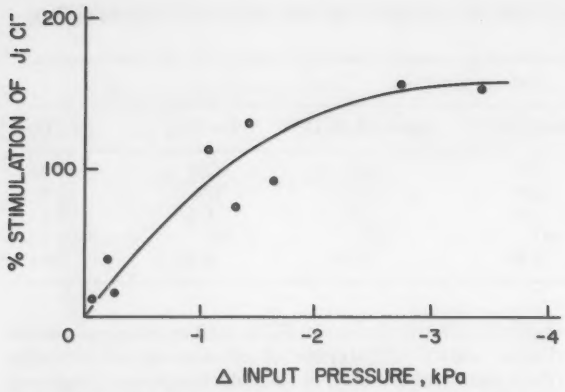

FIG. 5. Effect of decreasing input pressure on stimulation of Cl^- influx in the isolated, saline-perfused head of rainbow trout. The decreases in input pressure were caused by adding various concentrations of $NaHCO_3^-$ to the perfusate ($n = 9$). Curve was fitted by eye.

5 mmol/L and 13 mmol/L [HCO_3^-], Table 1). Altering perfusate [HCO_3^-] from 13 to 26 mmol/L or switching from "low" P_{CO_2} (187 Pa = 1.4 Torr) to 1 kPa (7.5 Torr) P_{CO_2} elicited changes in pH well within the normal physiological range; thus, input pressure and gill hemodynamics did not change.

The above results indicate that stimulation of branchial Cl^- uptake by perfusate $NaHCO_3^-$ may be due to accompanying hemodynamic changes and not necessarily to increased entry of HCO_3^- into the gill epithelium. As such, these results cannot confirm the model of Haswell et al. (1980), which suggests permeability of the basal membrane of gill epithelial cells to HCO_3^- and that plasma HCO_3^- is a major source for branchial Cl^-/HCO_3^- exchange. On the other hand, the results do support the more widely accepted model (Maetz 1971, 1974) wherein branchial carbonic anhydrase catalyses the hydration of plasma CO_2. The occurrence of Cl^- uptake in low HCO_3^- perfusate and the stimulatory effect of perfusate P_{CO_2} on Cl^- uptake can be explained by production of HCO_3^- by carbonic anhydrase catalysed CO_2 hydration. Similar confirmation for this role of carbonic anhydrase has come from the study of Payan and Matty (1975) who showed that Na^+/NH_4^+ exchange in the perfused head also is proportional to perfusate P_{CO_2}.

The results of our study and a previous one (Perry et al. 1982) indicate that the gill epithelium of rainbow trout is functionally impermeable to plasma HCO_3^- in terms of CO_2 excretion or ion exchange. In our opinion, the correct pattern of CO_2 movement across the gill involves entry of molecular CO_2 into gill epithelial cells and its subsequent hydration catalysed by carbonic anhydrase to yield HCO_3^- and H^+. In this manner the counter-ions for Cl^-/HCO_3^- and Na^+/NH_4^+ (H^+) exchanges are generated. CO_2 excretion is accomplished, in part, by apical Cl^-/HCO_3^- exchange but is mostly a result of diffusion of molecular CO_2 across the gill epithelium (Cameron 1976; Perry et al. 1981).

Acknowledgements

This study was performed while S.F.P. was a visiting scientist at the University of Nice, S.F.P. thanks everyone at Laboratoire de Physiologie Comparée, especially Professors Bornancin and Lahlou, for providing encouragement and support during the course of this work. We are grateful to Dr. D. J. Randall for critically reading the manuscript.

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Ambient pH and Calcium Concentration as Modifiers of Growth and Calcium Dynamics of Brook Trout, *Salvelinus fontinalis*

David W. Rodgers

Biological Research Section, Chemical Research Department, Ontario Hydro, 800 Kipling Avenue, Toronto, Ont. M8Z 5S4

Rodgers, D. W. 1984. Ambient pH and calcium concentration as modifiers of growth and calcium dynamics of brook trout, *Salvelinus fontinalis*. Can. J. Fish. Aquat. Sci. 41: 1774–1780.

Juvenile brook trout, *Salvelinus fontinalis*, were maintained in water of pH 5.3 or 6.5 and calcium concentrations of 5 or 40 mg/L to determine the effects of these factors on fish growth and calcium dynamics. Growth rates varied more than twofold and were significantly reduced by both low ambient calcium concentration and low pH. In contrast, calcium dynamics of the fish were significantly affected by calcium concentration but not pH. Brook trout in low-calcium water retained less labeled dietary calcium and deposited less labeled calcium in axial skeleton and visceral tissues than fish in high-calcium water. Calcium concentrations of the skin and fins were slightly but significantly reduced among fish in low-calcium water, but neither pH nor ambient calcium concentration significantly affected ash content or calcium concentration of axial skeleton and visceral tissues of experimental fish.

Nous avons conservé des ombles de fontaine (*Salvelinus fontinalis*) juvéniles dans de l'eau de pH variant de 5,3 à 6,5 et à teneur en calcium de 5 ou 40 mg/L afin d'étudier les effets de ces deux facteurs sur la croissance des poissons et la dynamique du calcium. Le taux de croissance a varié de plus du double, diminuant de façon significative lorsque la teneur de l'eau en calcium était faible ou que le pH était bas. Par contre, la concentration de calcium dans le milieu avait un effet significatif sur la dynamique de cet élément chez le poisson, mais non le pH. Les ombles gardées dans de l'eau à faible teneur en calcium retenaient moins de calcium alimentaire marqué et la quantité de calcium marqué retenue dans l'axe squelettique et les viscères était moindre que chez les poissons gardés dans une eau à forte teneur en calcium. La concentration de calcium dans la peau et les nageoires était légèrement, mais significativement, réduite chez les poissons gardés dans de l'eau à faible teneur en calcium mais ni le pH, ni la teneur du milieu en calcium n'ont influé de façon significative sur la teneur des cendres en calcium ou la concentration de calcium dans l'axe squelettique ou les viscères.

Received April 24, 1984
Accepted August 31, 1984
(J7763)

Reçu le 24 avril 1984
Accepté le 31 août 1984

The decline in abundance of fish populations in acid-stressed waters is among the best documented effects of acidic deposition on the aquatic environment (Beamish and Harvey 1972; Schofield 1976; Harvey et al. 1981). However, the mechanisms through which environmental acidification affects fish are less well known. In general, the effects of environmental acidification on fish populations are apparent in a range of pH (5.5–6.5) above that which is acutely toxic and thus represent a response to chronic rather than acute stress (Fromm 1980; Spry et al. 1981).

In acute exposure to low pH (<4.5), such as may occur with spring runoff, mortality appears to be caused by failure of ionic and osmotic regulation (Leivestad and Muniz 1976; McDonald 1983). In chronic exposure, however, teleosts generally tolerate pH as low as 5.0 with little apparent effect on ionic or osmotic concentrations (Fromm 1980; Lee et al. 1983). Thus, the chronic effects of environmental acidification do not appear to result from failure of ionic or osmotic regulation, although the energetic "costs" associated with regulation in the pH range of 5.0–6.0 may affect energy mobilization (Lee et al. 1983).

Recent studies in both the laboratory and field have noted apparent anomalies in calcium regulation of teleosts in acid-stressed environments. In laboratory studies, both urinary excretion of calcium ions and loss of surface bound calcium from the gills increase in salmonid fish exposed to low pH (McDonald and Wood 1981; McWilliams 1983). In field studies, Beamish et al. (1975) reported that in George Lake, an acid-stressed lake in the La Cloche Mountains, Ontario, female white sucker, *Catostomus commersoni*, did not display the normal prespawning surge in serum calcium concentrations that is associated with transport of yolk proteins in vitellogenesis (Dacke 1979). These fish did not appear to spawn successfully. White sucker from acid-stressed lakes, including George Lake, also had significantly lower calcium concentrations in the centra of their vertebrae than fish from near neutral lakes in the same region (Fraser and Harvey 1982). Further, white sucker from George Lake have shorter caudal vertebrae and some have deformed caudal fins, which may signify bone demineralization (Fraser and Harvey 1982). Calcium ions are central to a myriad of biological functions ranging from muscle contraction to maintenance of membrane permeability (Dacke 1979), and it is tempting to hypothesize that interference with calcium regulation is among the principal chronic effects of environmental acidification on fish.

Unfortunately, this hypothesis is largely confounded by the fact that the majority of these effects of acid stress on fish were observed in waters of low calcium concentration in addition to low pH. Calcium concentration has a marked influence on the

flux across the gills of both noncharged molecules (tritiated water) and ions (Na^+, H^+, and Cl^-), with changes in both active and passive transport processes implicated (Ogawa 1974; Isaia and Mansoni 1976; McWilliams and Potts 1978). Calcium concentration also affects the electrical potential of the gills (McWilliams and Potts 1978), the uptake and toxicity of pollutants (Sprague 1970; Rodgers and Beamish 1983), and the calcium permeability of the whole fish (Mayer-Gostan et al. 1983). Further, elevated calcium concentrations may mitigate the effects of low pH on fish (McDonald et al. 1980; Brown 1982; McWilliams 1982; McDonald 1983; McDonald et al. 1983). The relative contributions of calcium concentration and pH to apparent anomalies in calcium regulation in waters of low pH and calcium concentration thus remain to be resolved. I investigated the effects of calcium concentration and pH on growth and the dynamics of dietary calcium in brook trout, *Salvelinus fontinalis*.

Materials and Methods

Juvenile brook trout were obtained from a commercial hatchery (Glenwood Trout Hatchery, Ashburn, Ontario). Prior to experiments, fish were maintained in 400-L tanks supplied with dechlorinated Toronto tap water (15 ± 1°C, pH 7.5, 40 mg Ca/L) and fed to satiation with a commercial trout diet three times each week. Laboratory photoperiod was regulated to correspond to natural light regime, and increased from approximately 8 h light : 16 h dark in December to approximately 12 h light : 12 h dark in March.

For the experiments, trout (initial weight ~20 ± 5 g) were transferred to and maintained in 20-L plastic tanks at an initial density of 13 fish per tank. Tanks were contained in a temperature-regulated water bath (15 ± 1.0°C), aerated with compressed air, and supplied with water at 7.5 L/h with controlled calcium concentration (5 or 40 mg Ca/L) and pH (5.3 or 6.5). There were two replicate tanks for each of the four combinations of pH and calcium. Calcium concentrations of approximately 5 mg Ca/L and pH of 5.0–5.5 are typical of acid-stressed lakes (Harvey et al. 1981).

The trout were fed a specially prepared, low-calcium diet (Table 1) for 3 wk, fed this same diet labeled with ^{45}Ca for the next 4 wk, and then returned to the nonlabeled, low-calcium diet for the subsequent 4 wk. Fish were fed a ration of 1.5% wet wt/d for 5 d (Monday–Friday) and then not fed for the next 2 d. Fish were weighed and rations adjusted weekly.

At 3, 10, 17, and 31 d after last feeding of labeled diet, a sample of three fish was removed at random from each tank. These sampling periods are subsequently referred to as week 0, week 1, week 2, and week 4, respectively. Fish were killed by anesthetization in tricaine methane-sulphonate (MS222) solution (50 mg/L), weighed, and frozen (−20°C) in individual plastic bags for 2–4 wk until processed. Frozen fish were steamed in an autoclave for 3 min and then dissected to separate skin and fins, axial skeleton, and remaining tissues. Tissue samples were ashed at 700°C to constant weight, dissolved in nitric acid (5 mL), and then made up to constant volume (25 mL) with distilled water for analysis of stable and radioactive calcium.

Dechlorinated Toronto tap water was deionized using a commercial deionizer (Culligan, charcoal filter and 30-cm two-bed strong base) and supplied to two head tanks. Within the head tanks, a pH titrator regulated pH (using 0.1 mol H_2SO_4/L or NaOH as required) to maintain nominal pH's of either 5.3 or 6.5 in experimental tanks. A peristaltic pump delivered a salt solution containing sodium, potassium, and calcium chloride to the pH-regulated deionized water before delivery to experimental tanks. Nominal sodium and potassium concentrations were 4.0 and 0.5 mg/L, respectively, for all tanks; nominal calcium and chloride concentrations were 40 and 70 mg/L, respectively, for high-calcium tanks and 5 and 10 mg/L, respectively, for low-calcium tanks.

TABLE 1. Formulation of the test diet.

	%
Casein	40
Gelatin	5
Wheat gluten	5
Starch	15
α-Floc	9
Amino acid premix[a]	1
Vitamin premix[b]	2
Mineral premix[c]	8
Fish oil	15
Total	100

[a]Consisted of 50% L-methionine, 30% L-arginine, and 20% starch.
[b]Vitamin mix as in Hilton and Atkinson (1982).
[c]Mineral mix as in Hilton et al. (1980) but without $CaHPO_4 2H_2O$ and $CaCO_3$.

There was no mortality of experimental fish during the period of acclimation and feeding of experimental diet. Subsequent to the first sampling period (week 0) a system failure resulted in complete mortality of fish in pH 6.5, low-calcium tanks. In other tanks, there was no mortality until the last week when two fish in one of the pH 5.3, high-calcium tanks died. These fish displayed severe erosion of the caudal fin and caudal peduncle, which apparently resulted from persistent aggression by the dominant fish in the tank. Fish in all tanks fed well during the acclimation period and feeding of labeled diet. After the third sampling period (week 2), the apparent intensity of feeding of fish decreased, although all food was consumed. This change in feeding intensity appeared to correspond to an increase in aggression among fish within the tank, suggesting that at this low density (four fish per tank), fish became territorial and feeding of subordinate fish may have been suppressed.

Dissolved oxygen concentrations were always greater than 80% of air saturation and calcium concentrations maintained within 5% of nominal. Continuous recordings of pH in experimental tanks revealed diurnal variation in pH of approximately 0.3 and 0.2 pH unit in pH 5.3 and 6.5 tanks, respectively. These variations in pH apparently correspond to diurnal variations in rates of release of respiratory and excretory products by fish, with concomitant changes in buffering capacity of the experimental tanks. Actual pH was thus maintained within 0.3 pH unit of the 5.3 nominal for fish in the low-pH tanks and 0.2 pH unit of the 6.5 nominal for fish in the high-pH tanks. Ammonia concentrations were measured periodically and remained below 1 mg/L. Similarly, concentrations of a number of metals (<0.1 μg Cd/L; 3–8 μg Cu/L; <20 μg Mg/L; <5 μg Ni/L; 2–5 μg Pb/L; 80–90 μg Zn/L) were within limits suggested as conducive to optimum health of cold-water fish (Wedemeyer and Yusutake 1977).

The specially prepared low-calcium diet was formulated by

the Department of Nutrition, University of Guelph. The dry diet was mixed with 50% distilled water, extruded in a food mixer, lyophylized, and kept frozen in plastic bags until used. Diet labeled with ^{45}Ca was prepared in the same way but with approximately 40 MBq of ^{45}Ca-labeled $CaCl_2$ (specific activity 670 MBq/mg Ca, New England Nuclear, Montreal, Que.) added to the aqueous solution before mixing with 1.5 kg of diet. Calcium concentrations of labeled and nonlabeled diets were 5.37 ± 0.07 and 5.27 ± 0.06 mg Ca/g dry wt, respectively (mean ± SE, $n = 15$). The activity of the labeled diet at the time of first sampling was 1.70 ± 0.05 kBq/g ($n = 14$).

Routine determinations of calcium, pH, and dissolved oxygen of water in the test tanks were made using standard methods (APHA et al. 1981). Routine calcium measurements obtained by titration with EDTA agreed well with values obtained for the same samples using atomic absorption spectrometry. Calcium in tissue digests was determined by atomic absorption spectometry. ^{45}Ca was determined by scintillation counting of duplicate samples of acidified tissue ash using a Packard Tri-carb scintillation counter (model 300C) and Monophase 40 liquid scintillation cocktail. Results are expressed as activity per milligram of Ca and are corrected for background, quench, and radioactive decay. In water samples, Ca, Mg, Na, K, and Zn concentrations were determined by atomic absorption spectrometry (AAS) and Cd, Cu, Ni, and Pb were determined by AAS using a graphite furnace.

Growth rates were determined from the change in weight of all fish in the tank over the period that the fish were fed labeled diet. During this period, constant numbers of fish were maintained in all tanks, and fish fed avidly. Growth rates were determined from the difference between initial and final weights over the period and growth expressed as percentage of initial wet weight per day. The mean retention (percentage) of labeled dietary calcium was determined from the ratio of the quantity of labeled calcium consumed by fish to the total activity of fish within the tank.

Experiments were analyzed using the appropriate analysis of variance model. When repeated measurements were made on the same experimental unit (tank), the experiment was analyzed as a split plot in time using conservative degrees of freedom (Steele and Torrie 1960). Cell means were compared using the least significant difference with t and t' values calculated as appropriate (Steele and Torrie 1960), if the F-ratio was significant ($P < 0.05$). In all statistical tests of significance, differences between cell means were considered significant if $P \leq 0.05$. Visual inspection of residual and normal probability plots did not reveal apparent violations of statistical assumptions of normality and homogeneity of variance using raw data, and analyses were made without statistical transformation of data.

Results

During the 4 wk the trout were fed labeled diet, growth rates of the trout under different treatments varied more than twofold (Fig. 1). Both pH and calcium concentration significantly affected growth rate with no apparent interaction between factors. The average growth rate of fish maintained in water of high calcium concentration (1.38 ± 0.22% wet wt/d (mean ± SE)) was significantly greater than that of fish kept in water of low calcium concentrations (0.97 ± 0.14% wet wt/d). Similarly, the growth rate of fish at pH 6.5 was significantly higher than that of fish at pH 5.3 (1.47 ± 0.16 and 0.88 ± 0.11% wet wt/d, respectively).

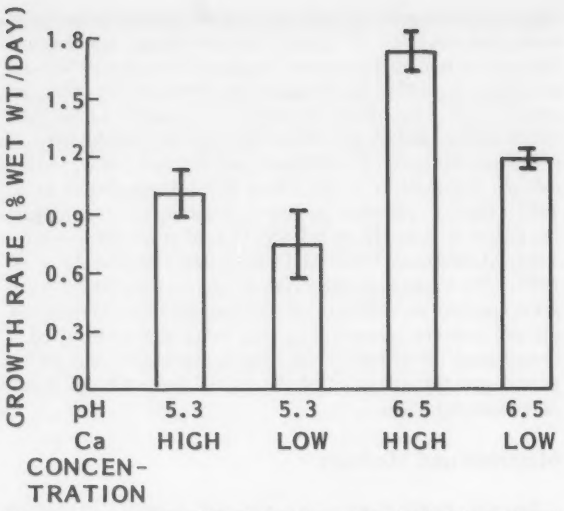

FIG. 1. Growth rate of brook trout in waters of pH 5.3 or 6.5 and calcium concentrations of 5 and 40 mg/L (mean ± SE, two tanks of 13 fish per treatment).

Ash content of the brook trout did not vary significantly with ambient calcium concentration, pH, or duration of the experiment. Mean ash content was 2.4 ± 0.2% wet wt. Similarly, average calcium concentrations of axial skeleton and remaining tissues (339 ± 2.8 and 79.8 ± 2.7 mg Ca/g ash, respectively) were stable throughout the experiment and not significantly affected by ambient calcium concentration, pH, or duration of the experiment (Table 2). In contrast, the calcium concentration of the skin and fins was significantly affected by the calcium concentration of the ambient water but not by pH or experimental duration. At week 0, the mean calcium concentration of skin and fins of trout in high-calcium water (304 ± 3.0 mg Ca/g ash) was significantly higher than that of fish in low-calcium water (294 ± 1.5 mg Ca/g ash).

Changes in the proportion of total calcium in each of the tissue compartments largely paralleled changes in calcium concentration. At week 0, the proportion of total calcium in skin and fins of fish maintained in water of high calcium concentration (49.0 ± 1.0%) was significantly greater than that of fish in water of low calcium concentration (45.7 ± 1.1%). The proportions of total calcium in axial skeleton and remaining tissues were stable throughout the experiment with average proportions of 39.7 ± 0.4% and 13.8 ± 0.5%, respectively.

Retention of ^{45}Ca in the labeled diet was significantly affected by calcium concentration but not by pH (Fig. 2). Mean retention of labeled calcium by fish in water of high calcium concentration (38.0 ± 1.6%) was significantly greater than retention of ^{45}Ca by fish in water of low calcium concentration (30.6 ± 1.6%).

Trends in variation of specific activity of each tissue compartment were examined separately, as changes in the distribution of radiolabeled calcium differed among tissues. The specific activity of the axial skeleton was significantly affected by ambient calcium concentration but not by pH or experimental duration (Table 3). At week 0, the mean specific activity of axial skeleton of trout in water of high calcium concentration (328 ± 30 Bq/mg Ca) was significantly greater than that of fish from low-calcium water (233 ± 22 Bq/mg Ca). A similar pattern was seen in the remaining tissues at week 0 with significantly higher

TABLE 2. Average calcium concentration (mg Ca/g ash) of tissues of brook trout maintained in waters of pH 5.3 or 6.5 and calcium concentrations of 5 or 40 mg Ca/L (mean ± SE, $n = 6$).

pH	[Ca] (mg/L)	Tissue	Days after last feeding of labeled diet			
			3	10	17	31
5.3	5	Skin	294±1	296±4	301±2	298±7
		Skeleton	335±4[a]	345±8	339±5	334±5
		Remains	81.7±7.3	79.6±7.6	86.4±7.3	73.0±6.3
5.3	40	Skin	307±2[a]	321±6	310±5	306±11
		Skeleton	345±4	343±6	350±4	342±9
		Remains	70.5±2.4	74.2±4.5[a]	79.3±5.3	83.1±8.0
6.5	5	Skin	294±3			
		Skeleton	335±5			
		Remains	75.5±6.6			
6.5	40	Skin	302±5	307±2	314±3	304±5
		Skeleton	326±6	340±5	342±11	335±3
		Remains	70.2±4.7	88.0±7.2	97.9±4.8	77.7±4.9

[a] $n = 5$.

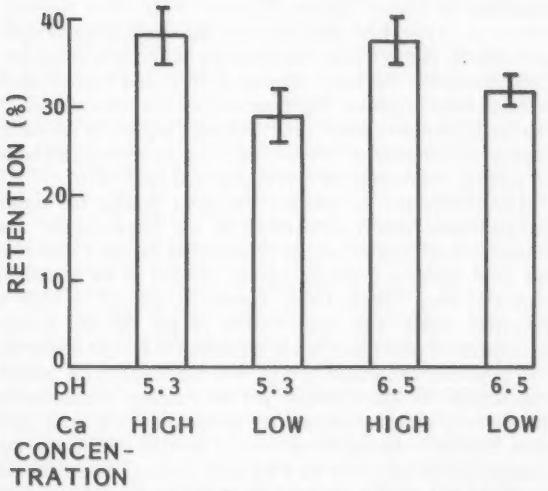

FIG. 2. Retention (% of total ^{45}Ca ingested) of dietary ^{45}Ca by brook trout in waters of pH 5.3 or 6.5 and calcium concentrations of 5 or 40 mg/L (mean ± SE, two tanks of 13 fish per treatment).

specific activities observed in fish from water of high calcium concentrations (mean activities of 462 ± 35 and 327 ± 33 Bq/mg Ca in waters of high and low calcium concentration, respectively). In addition, the specific activity of the remaining tissues decreased significantly with time after last feeding of labeled diet. Mean specific activity of the skin and fins also decreased significantly with time but was not significantly affected by pH or calcium concentration.

The differences in mobility of calcium within specific tissue compartments are reflected by the changes in specific activity with time. At week 0, the average specific activity of remaining tissues was significantly greater than that of skin and fins, which in turn had a significantly higher specific activity than the axial skeleton. In weeks 1 and 2, the mean specific activity of the remaining tissues was still significantly higher than that of both skin and fins, and axial skeleton, but the average specific activities of these two tissues were not significantly different. At week 4, differences in specific activity among tissues were not statistically significant.

Discussion

Both pH and calcium concentration significantly affected growth of brook trout. However, only calcium concentration significantly influenced calcium dynamics in the experimental fishes. These results thus indicate that over the range tested, pH had relatively little effect on calcium dynamics and skeletal growth. Conversely, ambient calcium concentration had a pronounced effect on calcium dynamics. Apparent anomalies in calcium regulation of fish in acid-stressed waters may thus result from factors other than pH alone, possibly the combined stresses of low calcium concentration, low pH, and elevated metal concentrations.

The consistent reduction in growth rate of fish at pH 5.3 relative to fish at pH 6.5 demonstrated that low pH reduced growth of brook trout fed fixed rations. Previous experimental studies of the effects of pH on fish growth reported either a reduction in growth at low pH or no effect. For alevins and adult brook trout fed ad libitum, Menendez (1976) reported that fish maintained at pH 4.5 and 5.0 grew more slowly than fish at pH 7.0. However, growth rates of yearling brown trout, *Salmo trutta*, fed fixed rations (2.9% body weight/d for 48 d) did not differ significantly among fish maintained at pH 6.26, 5.44, and 5.0 (Jacobsen 1977). In the present study, fish were fed fixed rations and consumed all food offered; thus, the reduction in growth observed for brook trout maintained at pH 5.3 is not merely an artifact of reduced appetite. Unfortunately, present information concerning the effects of pH on fish energetics is not sufficient to suggest the metabolic basis of reduced growth at low pH, although recent experiments of Lee et al. (1983) have implicated the increased costs of ionic and osmotic regulation at pH 5.0–6.0. Metabolic compensation to low pH may also be possible, as Menendez (1976) noted that growth rates of adult brook trout at pH 5.0 and 7.0 were not significantly different in the last 2 mo of his 5-mo study. The differences in response of brook and brown trout may also reflect species-specific differences in susceptibility to low pH.

TABLE 3. Average specific activity (Bq/mg Ca) of tissues of brook trout fed a diet labeled with ^{45}Ca and maintained in waters of different pH and calcium concentration (mean ± SE, $n = 6$).

pH	[Ca] (mg/L)	Tissue	Days after last feeding of labeled diet			
			3	10	17	31
5.3	5	Skin	258±47	189±32	164±25	200±35
		Skeleton	225±43	173±33	149±26	191±34
		Remains	305±56	247±40	199±33	221±38
5.3	40	Skin	338±53[a]	191±35	267±51	179±28
		Skeleton	322±46	192±41	270±49	184±27
		Remains	451±48	217±53	286±51	179±29
6.5	5	Skin	319±44			
		Skeleton	241±17			
		Remains	349±38			
6.5	40	Skin	317±63	222±49	279±46	264±9
		Skeleton	334±43	225±57	292±53	287±13
		Remains	473±56	276±62	292±47	279±12

[a] $n = 5$.

The reduction in growth rate of trout maintained in water of low calcium concentration indicates that under the conditions tested, a low ambient concentration of calcium may limit fish growth. This result was unexpected, as in previous studies with a number of species, dietary calcium concentrations ranging from 1 to 10 mg/g did not affect fish growth (Ogino and Takeda 1976, 1978; Watanabe et al. 1980; Ichii and Mugiya 1983), although a dietary calcium concentration of 15 mg/g was required for maximal growth in channel catfish, *Ictalurus punctatus* (Andrews et al. 1973). The above studies, however, were conducted in waters with a calcium concentration of approximately 20 mg/L or greater. At this concentration, increased calcium uptake from water appears to compensate for reduced dietary uptake (Ophel and Judd 1976; Ichii and Mugiya 1983). Unfortunately, although Wedemeyer and Yasutake (1977) recommended an alkalinity of at least 20 mg $CaCO_3$/L as conducive to optimal health of cold-water fishes, additional studies comparing the growth of fish maintained in waters of different calcium concentrations are not presently available. The dietary calcium concentration (5 mg Ca/g dry wt) used in the present study is low relative to that of commercial trout feeds (>10 mg Ca/g) and at the lower end of the range of 1–4 mg Ca/g wet wt (4–16 mg Ca/g dry wt assuming ~75% wet wt is water) reported for the diet of planktivorous fish (Berg 1968). Calcium concentrations of 4 mg/L or less are often reported for waters of lakes sensitive to acidification (Harvey et al. 1981); thus, in these environments, low concentrations of calcium in both food and water could limit fish growth.

The relative stability in ash content of the experimental fish is in accord with previous observations that ash fraction in salmonids is normally constant (Elliot 1976; Reinitz 1983). The observed ash content, 2.2–2.6% wet wt, is within the range of values previously reported for salmonid fishes of 2.6% wet wt for brown trout (Elliot 1976) and 2.0–2.7% wet wt for rainbow trout (Reinitz 1983). The proportions of total calcium in axial skeleton (~40%) and skin and fins (45–50%) are similar to those previously reported for teleosts (Simkiss 1974; Dacke 1979).

The slightly elevated calcium concentrations observed in skin and fins of trout in high-calcium water are consistent with previous studies indicating that the integument of teleosts is important to calcium uptake (Simkiss 1974). More recently, Flik et al. (1984) have identified the calcium-binding protein, calmodulin, in fish mucus. Interestingly, a decrease in calcium concentration of the water induced an increased concentration of calmodulin in mucus. The observed calcium concentration of the axial skeleton of brook trout (340 mg Ca/g ash) is similar to mean concentrations of 334–343 mg Ca/g ash reported for bone of goldfish, *Carassius auratus* (Ophel and Judd 1976).

The differences in calcium dynamics among the tissue compartments reflect differences in the physiological and metabolic functions of calcium in individual tissues. Calcium in the axial skeleton is predominantly utilized in the structural matrix of bone (Dacke 1979). Generally, calcium in bone is relatively stable with only 5–10% of the calcium readily exchangeable with tissue fluids (Simkiss 1974). The conservative behaviour of calcium in bone was confirmed in the present experiments in which neither pH nor calcium concentration significantly affected calcium concentration of the axial skeleton. Similarly, the specific activity of the axial skeleton did not change significantly over the 4 wk after feeding labeled diet. In contrast, the specific activities of both remaining tissues and skin and fins decreased significantly with time, reflecting mobilization or dilution of calcium within these pools. These differences in calcium dynamics among tissue components are consistent with differences in rate of turnover of calcium in guppies, *Lebistes* sp., where the biological half lives of ^{45}Ca in visceral tissue, muscle, and vertebrae were 3, 137, and 309 d, respectively (Rosenthal 1963).

The lower specific activity of both axial skeleton and remaining tissues of trout from low-calcium water at week 0 corresponds well with the lower retention of radiolabeled dietary calcium by these fish. This lower retention may derive from a decreased rate of uptake of dietary calcium or an increased rate of calcium efflux by fish in water of low calcium concentration. In a series of experiments using ^{85}Sr as a tracer of calcium and strontium uptake by goldfish, Berg (1968) indicated that at equivalent dietary calcium concentrations, a greater proportion of total calcium uptake is derived from dietary sources in waters of low calcium concentrations. Information concerning the effects of ambient calcium concentration on calcium efflux of fish is limited, although Phillips et al. (1957)

indicated that a greater proportion of labeled dietary calcium is excreted by brook trout in low-calcium water (5 mg/L) than in water of higher calcium concentration (50 mg/L). For a number of teleosts, flux across the gills of both noncharged molecules (tritiated water) and ions (Na^+, H^+, and Cl^-) increased at low ambient calcium concentrations (Ogawa 1974; Isaia and Mansoni 1976; McWilliams and Potts 1978). More recently, Mayer-Gostan et al. (1983) reported that both extraintestinal calcium influx and apparent calcium permeability increased in calcium-depleted killifish, *Fundulus heteroclitus*, maintained in calcium-deficient freshwater. Unfortunately, this study did not estimate calcim efflux. Available evidence thus suggests that at low ambient calcium concentrations, uptake of dietary calcium would increase rather than decrease, while calcium efflux may well increase. Accordingly, the lower retention of dietary calcium by brook trout in water of low calcium concentration is likely to result from an increased rate of loss of calcium from the fish rather than reduced uptake of dietary calcium. The lower specific activity of axial skeleton of trout in low-calcium water would result from less labeled calcium remaining available for deposition in bone. The reduced deposition of labeled dietary calcium did not affect total calcium concentration of the bone in the present short-term study; however, differences might become apparent in studies of a longer duration.

The lack of effect of pH on calcium dynamics seems contrary to field reports of reduced calcium concentrations in centra of vertebrae from white suckers caught in lakes of low pH and calcium concentration (Fraser and Harvey 1982). However, in the present study, only pH and calcium concentrations were varied, while in the field, elevated concentrations of metals (Al, Cd, Ca, Pb, Mn, Ni, and Zn) are frequently associated with low pH (Spry et al. 1981). Significantly, Fraser and Harvey (1982) reported elevated concentrations of manganese as well as reduced calcium concentration in centra of suckers from the most acid lake, George Lake (pH 4.65). Similarly, Moreau et al. (1983) reported that concentrations of manganese, zinc, and strontium in opercula and scales of brook trout from acidified lakes were significantly higher than the concentrations of these metals in fish from nonacidified lakes. Manganese-deficient rainbow trout display abnormal curvature of the backbone and tail (Ogino and Yang 1980), while deletion of manganese from the diet of carp, *Cyprinus carpio*, resulted in reduced calcium concentration in vertebrae (Satoh et al. 1983). The effects of excess manganese on fish have not been reported, but manganese poisoning has been suggested to alter calcium metabolism in humans (Chandra et al. 1974). It is thus probable that the apparent interference in calcium regulation observed in fish from recently acidified waters results from interactions among low pH, low calcium concentrations, and elevated metal concentrations. The nature of these interactions and the possibility of remedial actions have yet to be quantified.

Acknowledgements

The technical assistance of H. E. Kowalyk is gratefully acknowledged. I also thank Dr. J. Hilton, Department of Nutrition, University of Guelph, for providing experimental diet and advice.

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Postglacial Dispersal of Freshwater Fishes in the Québec Peninsula

Pierre Legendre

Département de Sciences biologiques, Université de Montréal, C.P. 6128, Succursale A, Montréal (Qué.). H3C 3J7

and Vianney Legendre

Service de la Faune, Ministère du Loisir, de la Chasse et de la Pêche, Gouvernement du Québec, 6255, 13ième Avenue Rosemont, Montréal (Qué.). H1X 3E6

Legendre, P., and V. Legendre. 1984. Postglacial dispersal of freshwater fishes in the Québec peninsula. Can. J. Fish. Aquat. Sci. 41: 1781–1802.

The possible postglacial dispersal of freshwater fishes in the Québec peninsula is described. We tested the hypothesis that fish dispersal was controlled more efficiently by movements of the earth crust and by morphological peculiarities of the peninsula than by upland divides presently found between river basins. Based on the actual distributions of 109 species of freshwater fishes, the presence and absence of these species was noted for each of 289 one-degree-square pixels of the peninsula. A geographical intermediate-linkage clustering was run with a spatial constraint, that is, only neighbouring pixels were allowed to cluster. Five main ichthyogeographic regions and 21 subregions were thus defined. The regional limits seem to be highly correlated with climatic, vegetational, and geomorphological limits or gradients. Knowing the fish species present in each subregion made it possible to deduce their pattern of postglacial dispersal, after computing a coefficient of dispersal direction between neighbouring subregions. The pattern of fish dispersal so derived assumes that the stenohaline species have crossed the centre of the peninsula. This can be explained by the isobasic movements since the end of the Wisconsin Ice Age, and also by a network of river headwater interconnections still extant today.

Cet article décrit la dispersion postglaciaire des poissons d'eau douce de la péninsule québécoise et tente de vérifier l'hypothèse selon laquelle la dispersion des poissons doit plus aux mouvements de l'écorce terrestre ainsi qu'à la géomorphologie particulière de ce territoire qu'aux limites d'altitude actuelles des différents bassins hydrographiques. Pour chacun des 289 pixels (ou : points d'image) d'un degré de côté qui couvrent la péninsule, la présence ou l'absence de 109 espèces de poissons d'eau douce fut notée à partir des cartes de répartition des espèces. Les pixels furent réunis en régions par groupement à liens intermédiaires avec une contrainte de contiguïté spatiale, ce qui signifie qu'on ne permettait qu'à des pixels voisins de se regrouper. Cinq régions ichthyogéographiques majeures, comprenant 21 sous-régions, furent ainsi définies. Les limites de ces régions semblent bien corrélées avec des limites ou des gradients climatiques, botaniques ou géomorphologiques. A partir des listes d'espèces présentes dans chaque sous-région, un coefficient de direction de la dispersion fut calculé entre sous-régions voisines pour déduire le schème général de la dispersion postglaciaire. Le schème ainsi trouvé suggère que plusieurs espèces sténohalines ont traversé la péninsule par son centre. Ceci peut s'expliquer par les mouvements des isobases depuis la fin de la glaciation du Wisconsin ainsi que par l'existence d'un réseau d'interconnexions entre les têtes des rivières. Ce réseau existe d'ailleurs toujours.

Received May 27, 1983
Accepted August 31, 1984
(J7380)

Reçu le 27 mai 1983
Accepté le 31 août 1984

The emerging field of quantitative biogeography has been reviewed by Crovello (1981), who discussed the 10 stages of biogeographic data analysis. This approach makes it possible to test various historical or ecological hypotheses regarding geographically distributed phenomena, using multidimensional data. The data sets may describe community composition, or the physical environment that the plants or animals live in. The various descriptors can be integrated through multidimensional analysis. This is more likely to bring answers to biogeographic problems than an analysis based on one descriptor at a time because of the interactions between ecological variables that are found in the real world. Examples of such studies have been reviewed by Peters (1971). Other methods have been used by Goodall (1974) for plant distribution data, and by Bock and Root (1981) for landbirds.

The ichthyogeographic knowledge of northeastern North American fresh waters began (Legendre 1963) with the explorations by Jacques Cartier (Pouliot 1934), Samuel Champlain (Laverdière 1870), and the Jesuits (Thwaites 1896–1901), but until recently, comprehensive biogeographic data had been compiled, for large areas of Québec, mostly in unpublished manuscripts by V. C. Wynne-Edwards, L. R. Richardson, V. D. Vladykov, and G. Préfontaine (Legendre 1971), except for the maps in Scott and Crossman (1973). The postglacial dispersal of a few species in western Québec was described by Dadswell (1972, 1974). On the other hand, interest in classification of waters for stocking purposes was manifest in

governmental offices since 1944 (Prévost 1944) and has extended to ecologists (Legendre et al. 1980). Legendre (1971) reviewed the literature available on Québec fish biogeography and summarized the research needed in the future. The present paper follows in these footsteps.

Our objective was to describe and explain the dispersal of freshwater fishes in the Québec peninsula since the last glaciation. The Laurentide Ice Sheet retreated from the peninsula from approximately 14 000 to 5000 yr ago. Since then the fish species reinvaded the territory; we understand that stenohaline species came northward from United States refugia through the Great Lakes, the province of Ontario, and New England states via some or all of the temporary postglacial southern watershed interconnections such as those illustrated by Prest (1970), while euryhaline species arrived mostly from the Atlantic and Arctic seas. Our main hypothesis is that species dispersal was controlled more efficiently by movements of the earth crust and by morphological peculiarities of the peninsula than by mountain ranges and other altitudinal limits presently found between river basins. It is then obvious that we cannot follow the example of Legendre and Beauvais (1978) or Bailey and Smith (1981) who took the river watershed as the basic Operational Geographic Unit (OGU: Crovello 1981) of their numerical analyses.

Our biogeographic analysis proceeds in three steps: (1) The peninsula is divided into faunistically homogeneous regions, on the basis of present distribution maps of fish species, and according to an objective clustering criterion. It will be shown that the limits of these empirical regions do correspond to various types of natural barriers, gradients, or limits. (2) Patterns of species dispersal between these relatively homogeneous regions are sought, using a numerical approach based on the present fish distributions. (3) A physical mechanism is proposed, in terms of a network of presently extant river interconnections, to explain the dispersal pattern suggested by the dispersal analysis results for stenohaline and for euryhaline species.

Materials and Methods

Distribution maps for 109 species of freshwater fishes, covering the Québec peninsula, were published by Bergeron and Brousseau (1981), following the recommendations of Legendre (1971) about basic compilations that were necessary to initiate a synthesis of Québec ichthyogeography. Although admittedly incomplete, these maps assemble almost all of the fish census data presently available for Québec.

Since we did not wish to impose the pattern of river watersheds as an a priori assumption onto the ichthyogeographic data, the territory under study was divided instead into 289 pixels ("picture cells") of 1° of longitude by 1° of latitude, and the presence or absence of each fish species was recorded for each pixel in a 289 × 109 data matrix.

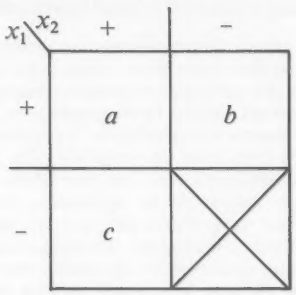
Clustering Procedure

The coefficient of Sørensen (1948) (see the first part of the formula for DD_2 in Table 1) was used to compute the similarity between all pairs of pixels on the basis of the fish presence–absence data, thus forming a 289 × 289 similarity matrix. Using this matrix, the pixels were clustered with a constraint of space contiguity, i.e. only neighbouring pixels were allowed to cluster, as proposed by several authors (Lefkovitch 1978, 1980; Lebart 1978; Monestiez 1978). As a clustering procedure, single linkage was discarded because surfaces were sought, rather than elongated dendrites of first-clustering pixels extending through the territory. On the other hand, complete linkage was also discarded to allow smooth gradients to be present in the resulting zoogeographic regions. Instead, an intermediate solution was used, and the pixels were clustered by a proportional-link linkage clustering algorithm, modified for the space contiguity constraint already mentioned. The connectedness required for the fusion of two clusters was Co = 50%. Details on the various methods of clustering available to ecologists can be found in Chapter 7 of Legendre and Legendre (1983).

The clustering program was designed to produce maps instead of the usual dendrograms. On each map (samples, Fig. 1), each contiguous cluster of pixels is represented by a different letter. A new map was produced for each level of similarity where clustering activity occurred.

Coefficient of Dispersal Direction

To determine the pattern of dispersal between the regions delineated by clustering, coefficients of dispersal direction were computed for all pairs of neighbouring regions, based on a comparison of their present fish faunas. The information to be compared for each pair of adjacent regions can be represented by the following 2 × 2 contingency table:



where a is the number of common species, b is the number of species exclusive to region x_1, and c is the number of species exclusive to region x_2.

Assumption 1: The species did not arise by evolution in situ. They dispersed into the territory in relatively recent geological time. The assumption is tenable for the whole of the Québec peninsula, where the inlandsis retreated between approximately 14 000 and 5000 yr ago (Andrews and Tyler 1977). It would make the forthcoming formulae useless, however, in areas where one could postulate local speciation among the fauna or flora under study. This could be the case with *Moxostoma hubbsi* (Legendre 1952, p. vi), which was stated to be endemic in Québec by Bailey and Smith (1981, p. 1555), an opinion to which we do not necessarily concur because postglacial times are seemingly too short for the production of a species presenting such elaborate anatomical differences in structures.

Assumption 2: Species dispersed in the past from regions of high to low species density, along present-day species gradients. Consequently, there are indications that a dominant flow of species dispersal occurred from a region x_1 to a region x_2: (2.1) if a good number of the species are common (value a above) and (2.2) if b is substantially larger than c (or the opposite).

When either of these conditions is not fulfilled, it does not

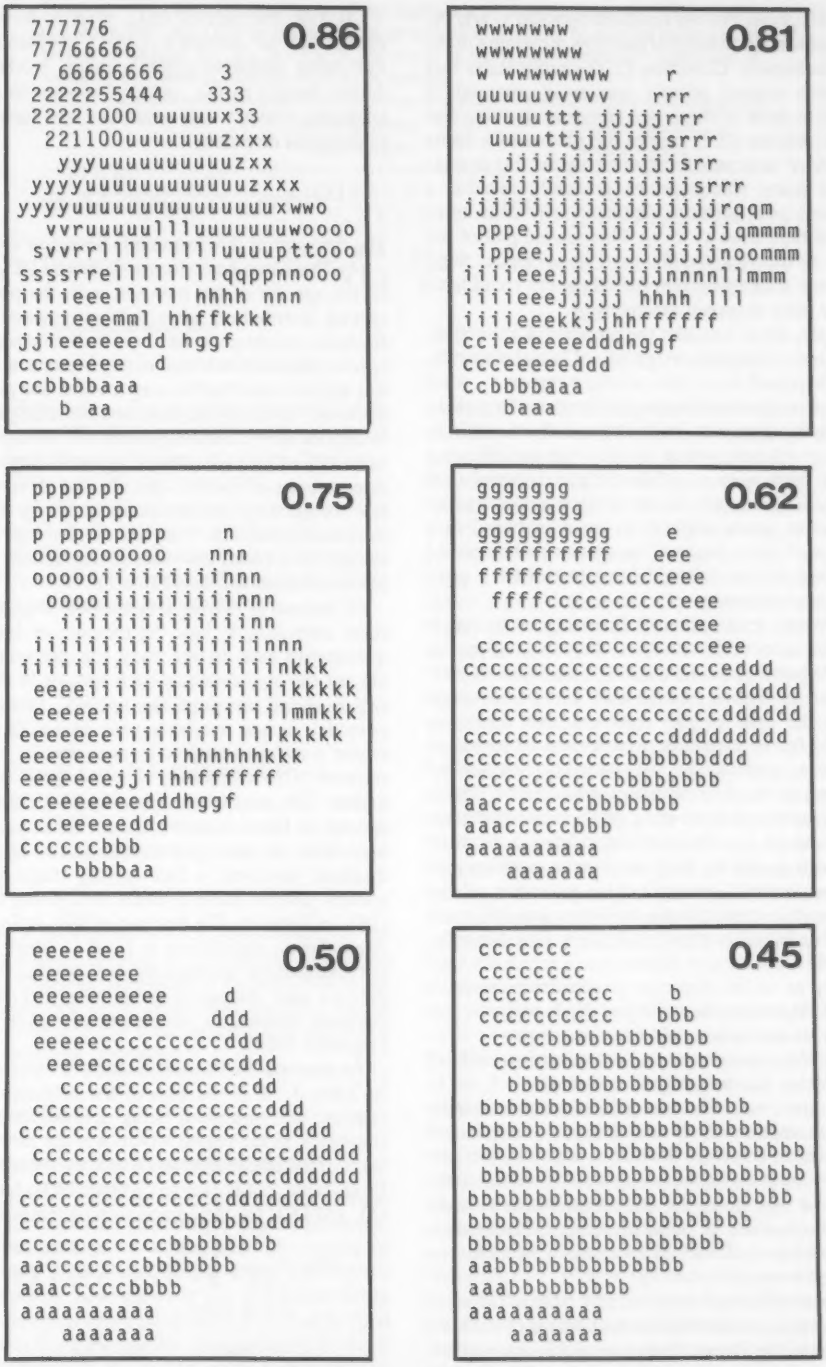


Fig. 1. Six of the maps produced by the biogeographic agglomerative clustering program. The level of similarity is shown on each map. Each group of pixels is represented by a different letter (beginning with *a* on each new map).

mean that a flow of species has not occurred between x_1 and x_2, but rather that there is no indication of that flow remaining in the present faunal distribution. Condition (2.1) simply states that unless two adjacent regions possess species in common, it would be difficult to think of these two faunas as deriving one from the other. Condition (2.2) creates the picture of a fauna "waiting at the border" to invade an adjacent region; this process must have taken place when species gradually invaded a recently deglaciated area, arriving simultaneously or in turn, from x_0 to x_1, and then from x_1 to x_2. This second part of the assumption is not as strong as the first part, since one can think of various situations where a present faunal pattern could have been produced by other dispersal mechanisms.

In a first example, let us consider the problem of extinction: suppose that a region x_1 contains two groups of faunal elements, a and c, which dispersed to a more northern region x_2, after which the group of c species disappeared from x_1. Region x_1 then contains only the a species, in common with x_2, while x_2 also contains the c species, which would seem to indicate a dispersal pressure from x_2 to x_1, while the true dispersal took place from x_1 to x_2. Fortunately, in the territory under investigation, this situation seems unlikely to have happened in a significant number of cases, because the species that dispersed far into deglaciated territory should have possessed a wide ecological valence or tolerance.

Another case where assumption (2.2) would be untrue is found in special instances of the situation where two regions, x_0 and x_1, have contributed to the formation of the fauna of their common neighbour x_2. Let us take the most complex example and suppose for the sake of the argument that region x_0 contained $(a + b)$ faunal elements, which were all passed to region x_2, and that x_1 contained $(a + c)$ faunal elements, all of which were passed to x_2. A comparison would show that x_2 now contains c elements unknown in x_0, while x_2 also possesses b elements unknown in x_1, which would indicate a dispersal flow from x_2 to both x_0 and x_1. Such an extreme situation may happen from time to time, giving a false indication of the dispersal direction. It is very unlikely, however, that this could occur in a large number of contiguous regions. Consequently, although any single set of species exclusive to a region does not give any certainty as to the direction of species dispersal, a general pattern of dispersal indicated by multiple region – pair comparisons over a wide area should be more reliable.

A *coefficient of dispersal direction*, with several variants of increasing complexity, can be designed as follows:

(1) Basic form: $a(b - c)$. The two quantities obtained independently from assumptions (2.1) and (2.2) are multiplied. If one wishes to visualize a species flow from region x_1 to x_2 by an arrow, then $(b - c)$ gives both the length and direction of the arrow (actually, the sign gives the direction), while a would give its width. If either one of these dispersal components is zero, then the arrow has a null surface area, which means that no migration occurred between x_1 and x_2.

(2) To make the coefficients comparable for pairs of faunas of different richness, each term should be standardized by dividing it by the richness of the fauna. This first usable form of the coefficient of dispersal direction will be called DD_1 and its formula is

$$DD_1 = \frac{a}{(a+b+c)} \frac{(b-c)}{(a+b+c)}$$

which can be thought of as the probability of passing from region x_1 to region x_2, for each species.

(3) The first part of DD_1, $a/(a + b + c)$, can easily be recognized as Jaccard's (1901) coefficient of community. Following Sørensen (1948), many workers prefer to give double weight to the common species in this assessment of similarity, which would result in a new form for the coefficient of dispersal direction:

$$DD_2 = \frac{2a}{(2a+b+c)} \frac{(b-c)}{(a+b+c)}.$$

The first part of this formula is Sørensen's coefficient.

(4) These two basic forms, DD_1 and DD_2, can be applied to all the species of the data set, with the possibility that some species distribution maps, whose contours have been drawn freehand, might generate some mathematical noise by giving a species presence in a region only because the shaded portion of this species' distribution map touches one pixel of the region in question. To avoid this problem, the same pair of equations can be applied only to species present, for example, in 25%, in 50%, or in 75% of the cells of each region. Computing them for these three subsets of species, and also for all species present, gives rise to eight ways of calculating the binary form of the dispersal direction coefficient. They are divided into those giving single weight (DD_1 form) and those giving double weight (DD_2 form) to the common species (Table 1).

(5) Instead of relying on presence–absence data, it might be more interesting to base the measure of dispersal direction on quantitative data. In our study, the quantitative data of interest are not the abundance of each species in the various regions, which would measure the species' success in the various potential niches available, but rather the fraction of each region's surface occupied by each species, taken as an indirect measure of the availability of both dispersion routes and suitable niches. The proportion of each region's pixels in which each species is found is presented in Table 2. These data can be assembled in two quantitative forms of the coefficient of dispersal direction: a form giving single weight to common species (DD_3 in Table 1) and a form giving them double weight (DD_4 in Table 1). The first part of DD_4 is Steinhaus' coefficient of similarity, also shown in Table 1, which is used to measure the resemblance between regions' faunas. If presence–absence data are used instead of quantitative data, Steinhaus' measure becomes Sørensen's coefficient of similarity (Legendre and Legendre 1983).

An example for the computation of these coefficients is given in Table 3. W is the sum of the minimum frequency for all species, this minimum being defined for each species as its frequency in the region where it is the rarest. A and B are the sums of the frequencies of all species in each of the two regions. From Table 3, it is easy to compute DD_3, Steinhaus' coefficient (S), and DD_4 for the comparison of regions 11 and 12:

$$DD_3 = \frac{W(A-B)}{(A+B-W)^2} = \frac{0.84(0.88-4.42)}{(0.88+4.42-0.84)^2} = -0.1495$$

$$S = \frac{2W}{(A+B)} = \frac{2 \times 0.84}{(0.88+4.42)} = 0.3170$$

$$DD_4 = S \times \frac{(A-B)}{(A+B-W)} = 0.3170 \times \frac{(0.88-4.42)}{(0.88+4.42-0.84)} = -0.2516.$$

TABLE 1. The four different forms of the coefficient of dispersal direction (DD) used in this study. DD_1 and DD_2 are computed for all species of a region, or only for those species present in at least 25, 50, or 75% of the pixels of the region. Steinhaus' coefficient of similarity (S), used to compare regions, is included.

	Common species: single weight	Common species: double weight
Presence–absence	$DD_1 = \frac{a(b-c)}{(a+b+c)^2}$	$DD_2 = \frac{2a}{(2a+b+c)} \frac{(b-c)}{(a+b+c)}$
Quantitative	$DD_3 = \frac{W(A-B)}{(A+B-W)^2}$	$DD_4 = \frac{2W}{(A+B)} \frac{(A-B)}{(A+B-W)}$
Quantitative similarity		$S = \frac{2W}{(A+B)}$

DD_3 and DD_4 show differences of scale, these two coefficients being largely monotonic. Finally, it can easily be shown that if presence–absence data are used instead of region frequency data, DD_3 becomes DD_1 and DD_4 becomes DD_2.

The binary forms of the coefficient open the way to a test of asymmetry of the 2 × 2 contingency table; this test is also known as the McNemar test. To test the null hypothesis that there is no asymmetry between two adjacent regions (H_0: $b = c$), we can compute the test statistic

$$X^2 = \frac{(b-c)^2}{(b+c)}$$

which is distributed as χ^2 with one degree of freedom. The log-linear form equivalent to this test is

$$X^2 = 2[b \ln b + c \ln c - (b+c) \ln ((b+c)/2)]$$

(Sokal and Rohlf 1981), which should be preferred to the first formula in the case of small values of b and c, as in the present study. In the formula, we replace $x \ln x$ by 0 when $x = 0$, since

$$\lim_{x \to 0} x \ln x = 0.$$

We will use it as a two-tailed test of significance of the difference between b and c, setting the probability of a type I error at $\alpha = 0.05$. If a specific hypothesis of dispersal was being tested (i.e. if the direction of an arrow was specified by the hypothesis and we wished to test if this arrow had a significant "length"), the test would be one-tailed.

Results and Discussion

Definition of Homogeneous Ichthyogeographic Regions

The dendrogram in Fig. 2 was drawn from the series of maps produced by the agglomerative clustering program (samples, Fig. 1). To limit the number of subregions, 21 clusters of contiguous pixels were picked out. No subregion was formed from less than three pixels. Also shown in Fig. 2 is the similarity level where each subregion aggregated at least 75% of its final number of pixels. On this dendrogram, the similarity levels of 0.50 and 0.70 were arbitrarily chosen to draw the map of regions (Fig. 3). Five clusters are well isolated at the 0.50 similarity level and define five main ichthyogeographic regions, blown apart in Fig. 3. The clusters isolated at the 0.70 similarity level represent main subregions, separated by full lines, while the clusters joining each other above the 0.70 similarity level represent minor regional components which are separated by broken lines. Clustering the pixels after removing the seven introduced species (I in Table 2) produced almost exactly the same dendrogram (Fig. 2), with only a few pixels being passed in three cases to adjacent minor subregions (those separated by broken lines in Fig. 3). In each major region, the subregions are numbered in a consecutive manner: region 1 (map 11 and 12): northern tundra; region 2 (map 21–23): east coast; region 3 (map 31–33): northwestern Gulf and estuary of St. Lawrence River; region 4 (map 41–43): upper St. Lawrence and Ottawa Valley (Champlain Sea area); region 5 (map 51–60): centre of the peninsula.

Since the limits of these ichthyogeographic regions do not correspond to the four major hydrographic watersheds of the peninsula (Hudson Bay, Ungava Bay, Atlantic Ocean, St. Lawrence River), the next question a biogeographer may ask is whether this partition of the territory makes sense, that is, do the dividing lines correspond to natural barriers, gradients, or limits? Notwithstanding the fact that a correlation does not imply a causality, this question was answered by looking at various physical or biological phenomena that were likely to influence the dispersal of fish species. Some of them, selected among other equally suggestive limits available in literature, are plotted in Fig. 4 and discussed hereafter.

Climatic gradients

(a) Region 1 (11 and 12) is separated from region 5 by the 16°C average maximum temperature in July (Wilson 1971). (b) This same climatic line corresponds to the northern portion of the division between subregions 21 and 53–54, while the southern portion of this same division corresponds to the isoline of lakes freezing over by November 20 (Wilson 1971). (c) Subregions 22 and 23 are separated from both 21 and 53 by the isoline of 810 mm annual precipitation (SEBJ 1978). (d) This same isoline also fits very well with the northern limit of subregion 55. (e) The dividing line between subregions 57–59 and 58–60 is close to the isoline of lake freeze-over by November 10 (Wilson 1971). (f) The growing season is shorter than 70 d above the northern limit of subregion 12 (Wilson 1971), which indicates severe climatic conditions. (g) Finally, the divisions between subregions 42, 31, and 32, as one goes down the St. Lawrence River, correspond very well to isolines of maximum summer temperatures (July and August; Houde 1978).

Geographic barriers

(a) Subregion 32 is bounded north of the St. Lawrence by a line of waterfalls, which prevent many euryhaline species from

TABLE 2. Fish distribution data from the maps of Bergeron and Brousseau (1981), divided into each species in the various pixels composing each region. Codes: S = stenohaline; E = euryhali

No. and species[a]	Code	11	12	21	22	23	31	32	3
Petromyzontidae									
1-*Ichthyomyzon fossor*	S	—	—	—	—	—	—	—	
2-*Ichthyomyzon unicuspis*	S	—	—	—	—	—	—	—	
3-*Lampetra appendix*	S	—	—	—	—	—	—	—	
4-*Petromyzon marinus*	E	—	—	—	26	57	86	100	1
Anguillidae									
5-*Anguilla rostrata*	E	—	—	—	84	—	100	100	1
Acipenseridae									
6-*Acipenser fulvescens*	S	—	—	—	—	—	43	—	
7-*Acipenser oxyrhynchus*	E	—	—	—	89	—	86	91	1
Amiidae									
8-*Amia calva*	S	—	—	—	—	—	—	—	
Lepisosteidae									
9-*Lepisosteus osseus*	S	—	—	—	—	—	14	—	
Hiodontidae									
10-*Hiodon alosoides*	S	—	—	—	—	—	—	—	
11-*Hiodon tergisus*	S	—	—	—	—	—	14	—	
Clupeidae									
12-*Alosa pseudoharengus*	E	—	—	—	—	—	86	91	1
13-*Alosa sapidissima*	E	—	—	—	—	—	71	91	1
14-*Dorosoma cepedianum*	S	—	—	—	—	—	57	—	
Salmonidae									
15-*Coregonus artedii*	S	4	—	—	—	—	57	—	
16-*Coregonus clupeaformis*	S	—	74	19	16	71	100	82	
17-*Coregonus nipigon*	S	—	—	—	—	—	—	—	
20-*Oncorhynchus kisutch*	I	—	—	—	—	—	—	—	
21-*Oncorhynchus nerka*	I	—	—	—	—	—	—	—	
23-*Prosopium cylindraceum*	S	4	42	38	26	100	71	9	
24-*Salmo clarki*	I	—	—	—	—	—	—	—	
25-*Salmo gairdneri*	I	—	—	—	—	—	14	18	
26-*Salmo salar*	E	4	—	100	100	100	100	100	1
27-*Salmo trutta*	I	—	—	—	—	—	—	—	
28-*Salvelinus fontinalis*	S	—	100	100	100	100	86	100	1
29-*Salvelinus namaycush*	S	60	100	63	16	14	100	55	
30-*Salvelinus salvelinus*	E	100	100	100	100	100	86	91	
Osmeridae									
32-*Osmerus mordax*	E	—	—	—	32	57	100	100	1
Umbridae									
33-*Umbra limi*	S	—	—	—	—	—	14	—	
Esocidae									
34-*Esox a. americanus*	S	—	—	—	—	—	—	—	
35-*Esox a. vermiculatus*	S	—	—	—	—	—	—	—	
36-*Esox lucius*	S	20	89	—	95	100	71	73	
37-*Esox masquinongy*	S	—	—	—	—	—	—	—	
38-*Esox niger*	S	—	—	—	—	—	—	—	

ided into the subregions of Fig. 3 (head of the columns). Data represent the percentage of presence of euryhaline; I = introduced.

32	33	41	42	43	51	52	53	54	55	56	57	58	59	60
—	—	—	29	—	—	—	—	—	—	—	—	—	—	—
—	—	8	43	—	—	—	—	—	—	—	—	—	—	—
—	—	—	71	—	—	—	—	—	—	—	—	—	—	—
100	100	—	57	33	—	—	—	—	3	—	—	—	—	—
100	100	75	100	100	—	—	2	—	—	—	—	—	—	6
—	—	100	100	—	—	—	—	—	—	100	100	100	100	89
91	100	—	43	—	—	—	3	—	—	—	—	—	—	—
—	—	8	86	—	—	—	—	—	—	—	—	—	—	—
—	—	58	71	—	—	—	—	—	—	—	—	—	—	—
—	—	33	—	—	—	—	—	—	—	—	—	100	—	—
—	—	100	57	—	—	—	—	—	—	—	—	78	—	—
91	100	—	57	—	—	—	—	—	—	—	—	—	—	—
91	100	—	57	—	—	—	—	—	—	—	—	—	—	—
—	—	—	57	33	—	—	—	—	—	—	—	—	—	—
—	—	100	71	100	33	91	58	—	69	100	100	100	100	100
82	—	100	100	100	100	91	98	100	100	100	100	100	100	100
—	—	—	—	—	—	55	—	—	—	100	100	89	—	—
—	—	—	14	—	—	—	—	—	—	—	—	—	—	—
—	—	—	14	—	—	—	—	—	—	—	—	—	—	—
9	—	42	57	33	100	64	100	100	100	80	20	—	100	89
—	—	—	43	—	—	—	—	—	—	—	—	—	—	—
18	43	17	100	33	—	—	—	—	—	—	—	—	—	—
100	100	17	71	67	17	—	71	100	52	—	—	—	—	17
—	—	17	100	100	—	—	—	—	—	—	—	—	—	—
100	100	100	100	100	100	100	100	100	100	100	100	100	100	100
55	14	83	100	100	100	91	100	100	100	100	—	11	100	94
91	29	17	43	—	100	82	55	100	7	—	20	—	—	28
100	100	58	100	100	—	—	—	—	24	—	—	—	—	50
—	—	50	100	33	—	—	—	—	—	—	—	—	—	—
—	—	—	29	—	—	—	—	—	—	—	—	—	—	—
—	—	—	14	—	—	—	—	—	—	—	—	—	—	—
73	—	100	100	100	100	100	100	100	100	100	100	100	100	100
—	—	75	100	33	—	—	—	—	—	—	—	—	—	—
—	—	—	29	33	—	—	—	—	—	—	—	—	—	—

TABLE 2. (*Continued*)

No. and species[a]	Code	11	12	21	22	23	31	32	3
Ictaluridae									
39-*Ictalurus natalis*	S	—	—	—	—	—	—	—	
40-*Ictalurus nebulosus*	S	—	—	—	—	—	14	—	
41-*Ictalurus punctatus*	S	—	—	—	—	—	—	—	
42-*Noturus flavus*	S	—	—	—	—	—	—	—	
43-*Noturus gyrinus*	S	—	—	—	—	—	—	—	
44-*Noturus insignis*	S	—	—	—	—	—	—	—	
Catostomidae									
45-*Carpiodes cyprinus*	S	—	—	—	—	—	—	—	
46-*Catostomus catostomus*	S	—	5	100	21	29	100	82	
47-*Catostomus commersoni*	S	—	—	—	—	29	86	64	
48-*Moxostoma anisurum*	S	—	—	—	—	—	—	—	
49-*Moxostoma carinatum*	S	—	—	—	—	—	—	—	
50-*Moxostoma hubbsi*	S	—	—	—	—	—	—	—	
51-*Moxostoma macrolepidotum*	S	—	—	—	—	—	—	—	
52-*Moxostoma valenciennesi*	S	—	—	—	—	—	—	—	
Cyprinidae									
53-*Carassius auratus*	I	—	—	—	—	—	—	—	
56-*Couesius plumbeus*	S	—	—	—	26	86	71	100	
57-*Cyprinus carpio*	I	—	—	—	—	—	29	—	
58-*Exoglossum maxillingua*	S	—	—	—	—	—	14	—	
59-*Hybognathus hankinsoni*	S	—	—	—	—	—	—	—	
60-*Hybognathus nuchalis*	S	—	—	—	—	—	—	—	
61-*Notemigonus crysoleucas*	S	—	—	—	—	—	100	18	
62-*Notropis atherinoides*	S	—	—	—	—	—	—	—	
63-*Notropis bifrenatus*	S	—	—	—	—	—	—	—	
64-*Notropis cornutus*	S	—	—	—	—	—	43	18	
65-*Notropis heterodon*	S	—	—	—	—	—	—	—	
66-*Notropis heterolepis*	S	—	—	—	—	—	29	—	
67-*Notropis hudsonius*	S	—	—	—	—	—	—	—	
68-*Notropis rubellus*	S	—	—	—	—	—	—	—	
69-*Notropis spilopterus*	S	—	—	—	—	—	—	—	
70-*Notropis stramineus*	S	—	—	—	—	—	—	—	
71-*Notropis volucellus*	S	—	—	—	—	—	—	—	
72-*Pimephales notatus*	S	—	—	—	—	—	—	—	
73-*Pimephales promelas*	S	—	—	—	—	—	—	—	
74-*Rhinichthys atratulus*	S	—	—	—	—	—	57	18	
75-*Rhinichthys cataractae*	S	—	—	—	—	71	100	45	
76-*Semotilus atromaculatus*	S	—	—	—	—	—	100	27	
77-*Semotilus corporalis*	S	—	—	—	—	—	71	—	
78-*Semotilus margarita*	S	—	—	—	—	—	100	73	
Gadidae									
79-*Lota lota*	S	—	—	—	—	—	100	18	
80-*Microgadus tomcod*	E	—	—	—	100	—	86	100	

32	33	41	42	43	51	52	53	54	55	56	57	58	59	60
—	—	—	14	—	—	—	—	—	—	—	—	—	—	—
—	—	50	100	100	—	—	—	—	—	—	—	—	—	—
—	—	42	86	—	—	—	—	—	—	—	—	—	—	—
—	—	—	71	—	—	—	—	—	—	—	—	—	—	—
—	—	8	57	—	—	—	—	—	—	—	—	—	—	—
—	—	8	—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	57	—	—	—	—	—	—	—	—	—	—	—
82	—	100	100	100	100	100	100	100	100	100	100	100	100	100
64	—	100	100	100	17	100	98	100	100	100	100	100	100	100
—	—	8	86	33	—	—	—	—	—	—	—	—	—	—
—	—	—	29	—	—	—	—	—	—	—	—	—	—	—
—	—	—	43	—	—	—	—	—	—	—	—	—	—	—
—	—	50	100	—	—	9	—	—	—	20	—	11	—	—
—	—	25	86	—	—	—	—	—	—	—	—	—	—	—
—	—	—	29	33	—	—	—	—	—	—	—	—	—	—
100	14	100	86	67	100	—	98	33	100	40	40	100	80	100
—	—	8	86	—	—	—	—	—	—	—	—	—	—	—
—	—	8	71	33	—	—	—	—	—	—	—	—	—	—
—	—	83	86	—	—	—	—	—	—	—	—	—	—	—
—	—	17	86	33	—	—	—	—	—	—	—	—	—	—
18	—	100	100	100	—	—	—	—	7	—	—	11	—	17
—	—	100	100	—	—	—	—	—	—	40	—	11	—	11
—	—	—	57	—	—	—	—	—	—	—	—	—	—	—
18	—	100	100	100	—	—	—	—	—	—	—	—	—	33
—	—	8	43	—	—	—	—	—	—	—	—	—	—	—
—	—	100	100	33	—	—	—	—	—	—	—	—	—	—
—	—	83	100	—	—	—	—	—	—	60	20	11	—	6
—	—	42	100	33	—	—	—	—	—	—	—	—	—	—
—	—	8	86	—	—	—	—	—	—	—	—	—	—	—
—	—	—	86	33	—	—	—	—	—	—	—	—	—	—
—	—	83	100	—	—	—	—	—	—	—	—	—	—	—
—	—	50	100	33	—	—	—	—	—	—	—	—	—	—
—	—	100	100	100	—	—	—	—	—	—	—	—	—	—
18	—	8	86	100	—	—	—	—	—	—	—	—	—	22
45	—	100	100	100	17	100	92	67	100	100	100	100	100	100
27	—	83	100	100	—	—	—	—	7	—	—	22	—	94
—	—	100	100	100	—	—	—	—	7	40	100	100	60	100
73	—	100	100	100	—	—	9	—	100	20	40	100	80	100
18	—	100	100	100	50	100	91	67	100	100	100	100	100	100
100	100	—	29	—	—	—	3	—	—	—	—	—	—	11

TABLE 2. (*Concluded*)

No. and species[a]	Code	11	12	21	22	23	31	32	3
Gasterosteidae									
81-*Apeltes quadracus*	E	—	—	—	—	—	43	100	10
82-*Culaea inconstans*	S	—	—	—	—	—	86	—	—
83-*Gasterosteus aculeatus*	E	100	84	100	100	86	100	100	10
84-*Gasterosteus wheatlandi*	E	—	—	—	5	—	57	27	5
85-*Pungitius pungitius*	E	100	100	100	100	100	100	100	10
Cyprinodontidae									
86-*Fundulus diaphanus*	S	—	—	—	—	—	57	18	2
87-*Fundulus heteroclitus*	E	—	—	—	—	—	—	—	5
Percopsidae									
88-*Percopsis omiscomaycus*	S	—	—	—	—	—	29	—	—
Atherinidae									
89-*Labidesthes sicculus*	S	—	—	—	—	—	—	—	—
Percichthyidae									
90-*Morone americana*	E	—	—	—	—	—	—	—	—
91-*Morone chrysops*	S	—	—	—	—	—	—	—	—
92-*Morone saxatilis*	E	—	—	—	—	—	86	45	5
Centrarchidae									
93-*Ambloplites rupestris*	S	—	—	—	—	—	—	—	—
94-*Lepomis gibbosus*	S	—	—	—	—	—	—	—	—
95-*Lepomis macrochirus*	S	—	—	—	—	—	—	—	—
96-*Lepomis megalotis*	S	—	—	—	—	—	—	—	—
97-*Micropterus dolomieui*	S	—	—	—	—	—	14	—	—
98-*Micropterus salmoides*	S	—	—	—	—	—	—	—	—
99-*Pomoxis nigromaculatus*	S	—	—	—	—	—	—	—	—
Percidae									
100-*Ammocrypta pellucida*	S	—	—	—	—	—	—	—	—
101-*Etheostoma caeruleum*	S	—	—	—	—	—	—	—	—
102-*Etheostoma exile*	S	—	—	—	—	—	—	—	—
103-*Etheostoma flabellare*	S	—	—	—	—	—	—	—	—
104-*Etheostoma nigrum*	S	—	—	—	—	—	29	—	—
105-*Etheostoma olmstedi*	S	—	—	—	—	—	—	—	—
106-*Perca fluviatilis*	S	—	—	—	—	—	100	9	—
107-*Percina caprodes*	S	—	—	—	—	—	57	9	—
108-*Percina copelandi*	S	—	—	—	—	—	—	—	—
109-*Stizostedion canadense*	S	—	—	—	—	—	—	—	—
110-*Stizostedion vitreum*	S	—	—	—	—	—	—	—	—
Sciaenidae									
111-*Aplodinotus grunniens*	S	—	—	—	—	—	—	—	—
Cottidae									
112-*Cottus bairdi*	S	—	16	6	11	—	29	—	—
113-*Cottus cognatus*	S	—	16	—	11	29	86	64	—
114-*Cottus ricei*	S	—	—	—	—	—	29	—	—
115-*Myoxocephalus quadricornis*	E	4	21	19	—	—	—	—	—

[a]Species of the Québec ichthyofauna whose distribution is not given in Bergeron and Brousseau *tshawytscha*; 31-*Thymallus arcticus* (extinct); 54-*Chrosomus eos*; 55-*Chrosomus neogaeus*.

32	33	41	42	43	51	52	53	54	55	56	57	58	59	60
00	100	—	14	33	—	—	—	—	3	—	—	—	—	—
—	—	100	100	100	—	—	—	—	14	20	100	100	40	100
00	100	42	71	33	17	91	62	67	14	100	100	33	—	44
27	57	—	—	—	—	—	—	—	—	—	—	—	—	—
00	100	100	86	33	100	100	100	100	100	100	100	100	100	100
18	29	8	86	33	—	—	—	—	—	—	—	—	—	—
—	57	—	—	—	—	—	—	—	—	—	—	—	—	—
—	—	100	100	33	—	—	—	—	—	80	80	100	—	100
—	—	—	29	—	—	—	—	—	—	—	—	—	—	—
—	—	—	71	—	—	—	—	—	—	—	—	—	—	—
—	—	—	57	—	—	—	—	—	—	—	—	—	—	—
45	57	—	57	33	—	—	—	—	—	—	—	—	—	—
—	—	92	100	67	—	—	—	—	—	—	—	—	—	—
—	—	83	100	67	—	—	—	—	—	—	—	—	—	—
—	—	—	43	—	—	—	—	—	—	—	—	—	—	—
—	—	8	43	—	—	—	—	—	—	—	—	—	—	—
—	—	75	100	100	—	—	—	—	—	—	—	—	—	6
—	—	50	100	—	—	—	—	—	—	—	—	—	—	—
—	—	8	71	—	—	—	—	—	—	—	—	—	—	—
—	—	—	29	—	—	—	—	—	—	—	—	—	—	—
—	—	—	14	—	—	—	—	—	—	—	—	—	—	—
—	—	100	86	33	—	—	—	—	—	—	—	—	—	11
—	—	25	100	33	—	—	—	—	—	—	—	—	—	—
—	—	42	100	67	—	—	—	—	—	—	—	—	—	—
—	—	—	57	33	—	—	—	—	—	—	—	—	—	—
9	—	100	100	100	—	—	—	—	—	100	100	100	40	100
9	—	100	100	33	—	—	2	—	7	60	—	44	—	44
—	—	—	86	—	—	—	—	—	—	—	—	—	—	—
—	—	75	86	—	—	—	—	—	—	—	60	100	—	—
—	—	100	100	100	—	36	2	—	10	100	100	100	100	94
—	—	67	86	—	—	—	—	—	—	—	—	—	—	—
—	—	100	86	33	83	100	88	—	7	100	100	100	100	94
64	—	100	100	100	—	100	98	—	100	100	100	100	100	100
—	—	92	43	67	—	—	—	—	3	—	—	33	—	94
—	—	8	—	—	—	9	3	—	—	20	20	—	—	—

rousseau (1981): 18-*Hucho hucho* (extinct); 19-*Oncorhynchus gorbuscha* (extinct); 22-*Oncorhynchus eus*.

TABLE 3. Data for the computation of coefficients DD_3, DD_4, as well as Steinhaus' similarity. Comparison of subregions 11 and 12: data from Table 2. The body of the table shows the relative frequencies of the nine stenohaline species present in these two ichthyogeographic subregions.

Region	Species code									Sum for x_{11} A	Sum for x_{12} B	Sum of minima W
	15	16	23	28	29	36	46	112	113			
x_{11}	0.04	0	0.04	0	0.60	0.20	0	0	0	0.88		
x_{12}	0	0.74	0.42	1	1	0.89	0.05	0.16	0.16		4.42	
Minimum	0	0	0.04	0	0.60	0.20	0	0	0			0.84

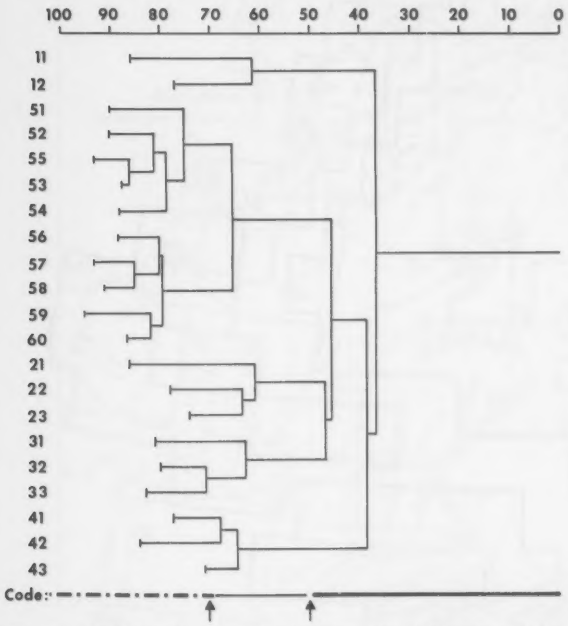


FIG. 2. Dendrogram of pixel clustering into ichthyogeographic regions. The arm corresponding to each region is shown only from the similarity level where 75% of its pixels are clustered. The division code for Fig. 3 is shown below the dendrogram.

going upriver. In small rivers, the falls actually lie to the south of this line, closer to the Gulf coast. Larger rivers are located in much wider and deeper valleys dug out by glaciers, so that the waterfalls are farther inland, usually north of 51°N. (b) On the other hand, the two highest mountain chains of the Québec peninsula (Otish, Torngat, Fig. 4) seem to have had little effect on the present distribution pattern of the fish species. They may, however, have had an influence on the dispersal routes, as will be discussed later.

Geomorphological limits

(a) Subregions 41, 42, and 43 are related to one another hydrologically and climatologically, and also because they share the effects of postglacial outlets of Lake Huron and the Champlain Sea postglacial transgression (Anonymous 1970) (not drawn in Fig. 4). This transgression left most of the lowlands of region 4 covered with marine sediments. (b) The line separating subregions 52, 56, and 57 on the one hand from 53 and 59 on the other corresponds to the limit of the surface deposits left by the Tyrrell Sea marine transgression (Anonymous 1970). Indeed, one of the isobase maps published by Andrews and Tyler (1977) shows that after the retreat of the ice margin, the northern limit of James Bay had, 6000 yr B.P., an altitude about 150 m lower than present, thus allowing the extension of this marine transgression. The marine sediments create in these subregions chemical (ions) and physical (turbidity) water conditions very different from those occurring in the Laurentide Shield plateau area (53, 55, 59), conditions that have in turn a strong influence on the composition of the fish community, as previously discussed (Legendre and Beauvais 1978; Legendre et al. 1980).

Vegetation

Subregions 51 and 53 are separated by the Arctic tree line (trees are still found, however, along Leaf River, which runs across subregion 51). Subregion 51 is then mostly a tundra habitat, yet somewhat warmer than the tundra subregions 11 and 12.

Thus, the ichthyogeographic regions delineated by the clustering procedure seem to hold, being apparently related to factors that could have influenced fish dispersal. The enumeration of potentially explanatory factors above also suggests that it would be interesting to test the species concerned (Table 2) for these same factors, under laboratory conditions.

Postglacial Dispersal Pattern

As already delineated, the ichthyogeographic regions appear to have a relative, internal homogeneity. On that basis, a definition of the pattern of fish postglacial dispersal may be attempted, using the various forms of the coefficient of dispersal direction described under Materials and Methods. It should be remembered that, given two adjacent fish faunas, a single value of this coefficient does not guarantee that dispersal did occur as described by this coefficient value; it merely indicates a possibility that the events occurred in this way. The overall picture produced by combining many values of this coefficient may, however, be considered as a stronger reconstruction of the postglacial dispersal history.

For each pair of adjacent subregions, 10 versions of the coefficient of dispersal direction were computed, as explained under Materials and Methods (the qualitative forms DD_1 and DD_2 for the species present in at least 1, 25, 50, and 75% of each region, respectively, and then the quantitative forms DD_3 and DD_4). In all but three cases, there was no contradiction of sign (the sign gives the direction of the dispersal arrow) between the 10 versions, for the coefficients that were retained as significant (see Fig. 5 and 7 and the following discussion).

To plot maps, it is necessary to select one version of the coefficient that best represents all the others. This selection was made on the basis of matrix correlations (also known as cophenetic correlations), computed with Pearson's r linear correlation and with Spearman's r rank-order correlation

FIG. 3. Map of ichthyogeographic regions (breaks) and subregions of the Québec peninsula. Hierarchy of divisions: break > full lines > broken lines. The similarity levels corresponding to these division codes can be found on Fig. 2.

coefficients, between all pairs of versions of the coefficient DD. Details on this method can be found in Sokal and Rohlf (1962) and in Legendre and Legendre (1983). In all cases, the correlation between the version giving single weight and that giving double weight to the common species is very high. On the other hand, the quantitative versions (DD_3 and DD_4) rank first in their ability to represent all the other versions of the coefficient, followed by the binary versions computed on the species present in 50% of the cells, followed closely in turn by the binary versions computed on the species present in 25% of the cells. The two more extreme versions (frequency larger than or equal to 75% and larger than 0%) are far less efficient in rendering the variations of all the other versions. Among the quantitative versions of the coefficient, DD_4 is preferred because it is easier to compare with Steinhaus' coefficient of similarity between regions, both giving double weight to the common species.

The test of significance of the direction, developed at the end of the Materials and Methods section, can be applied only to data in binary form. Using again the matrix correlation approach, we found that the binary versions of the coefficient that most closely resemble the quantitative versions (higher Pearson and Spearman correlations) were those computed from the species present in at least 50% of the cells, followed very closely by the versions computed from the species present in at least 25% of the cells. Thus, the test of asymmetry was applied to 2 × 2 contingency tables made, on the one hand, of the species present in at least 50% of the cells of each region and, on

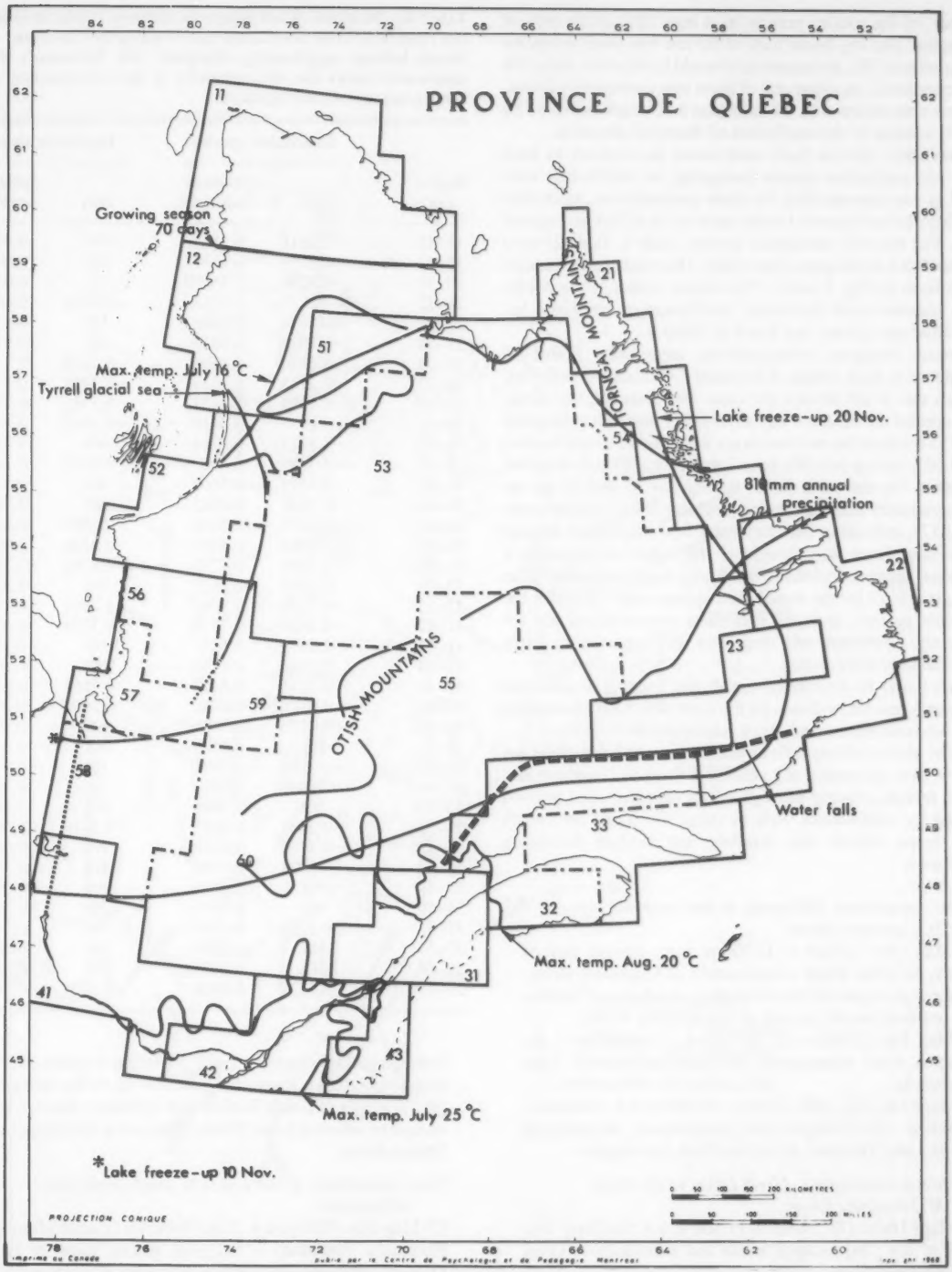


FIG. 4. Various types of natural barriers, gradients, or limits drawn on the map of the 21 ichthyogeographic subregions. See explanations in the text. The heavy broken line shows the general location of a line of waterfalls bounding subregion 32 north of the St. Lawrence.

the other, of the species present in at least 25% of the cells of each region. The log-linear form of the test was used. When the null hypothesis (H_0: no asymmetry) could be rejected, at the 5% confidence level, on either one of these two contingency tables, an arrow was drawn with the direction and length provided by the DD_4 version of the coefficient of dispersal direction.

Stenohaline species (here understood as confined to fresh water) and euryhaline species (seagoing, or indifferent) were treated as two separate files for these computations, since they were likely to have acceded to the territory by different dispersal routes. The recently introduced species (code I, Table 2) were not considered in this part of the study. The results are presented in map form in Fig. 5 and 7. The actual values of the coefficients, together with Steinhaus' coefficient of similarity between adjacent regions, are listed in Table 4.

In most instances, nonsignificant asymmetry (Table 4) corresponds to high values of Steinhaus' similarity coefficient, although this is not always the case. For instance, the stenohaline species do not show any asymmetry between subregions 53 and 55 because the two faunas are very similar to one another ($S = 0.90$), having possibly been formed by the same dispersal movement. On the other hand, subregions 21 and 22 do not show asymmetry although their faunal similarity is rather weak ($S = 0.57$), indicating that they have few stenohaline species in common. Over all subregions, the value of Pearson's r correlation between Steinhaus' similarity and the absolute value of DD_4 is -0.53 for the stenohaline species and -0.69 for the euryhaline species, showing that these two measures are not completely correlated and thus may be expected to carry complementary information.

Figure 5 may be interpreted as follows, keeping in mind that there is only one arrow drawn (at the most pictorially convenient place) between any two adjacent subregions.

(a) The glacial history tells us that the stenohaline species are likely to have reinvaded the peninsula from the southern and western refugia, mainly through routes (double-tailed arrows) provided by connections such as those illustrated on Prest's (1970) maps, whose map numbers are used in discussing connections.

South connections, tributaries to the southshore St. Lawrence River:

(1) Map 16e: 12 800 – 12 700 yr B.P.; toward Bay of Fundy, St. John River – headwaters of Chaudière River, via a marginal glacial lake in Québec, southeast of Québec city (outflow traced on map of Anonymous 1970).

(2) Map 16e: 12 800 – 12 700 yr B.P.; Connecticut – St. François river connection, via marginal glacial Lake Sherbrooke.

(3) Maps 16f, 16g, 16h: 12 500 – 12 000 yr B.P.; Hudson – Richelieu – St. François river connections, via marginal glacial Lake Vermont, in various Fort Ann stages.

Southwest connections, Great Lakes to the main St. Lawrence River:

(4) Maps 16a to 16j: 14 000 – 11 500 yr B.P.; and map 16x: 6000 yr B.P.; Mississippi River and tributaries – Great Lakes connections.

(5) Maps 16b, 16c: 13 600 – 13 200 yr B.P.; Susquehanna River – marginal glacial Finger Lakes (Newberry Lake), later tributaries to Lake Ontario.

West connection, Great Lakes to the Ottawa River:

(6) Maps 16k to 16x: 11 200 – 6000 yr B.P.; Lake Huron (various glacial stages) – Lake Nipissing (various glacial stages) – Ottawa River; connections up to the marginal glacial stages of Lakes Barlow and Ojibway–Barlow, one vestige of which is Lake Témiscamingue at the head of the Ottawa River.

West connection, Great Lakes to south James Bay tributaries:

(7) Map 16p: 9500 yr B.P.; Lake Superior (glacial Minong–Houghton transition) – marginal glacial stage of Lake Ojibway–Barlow, one vestige of which is Lake Abitibi, tributary to James Bay.

(b) On the south shore of the St. Lawrence River, the dispersal coefficient shows the species progressing to the Eastern Townships (43) and to the tip of the Gaspé peninsula (33).

TABLE 4. Measures of fish postglacial dispersal (using the quantitative form DD_4 of the coefficient) and of similarity (Steinhaus' coefficient) between neighbouring subregions. NS: McNemar's test of significance shows that the asymmetry in the corresponding 2×2 contingency table is not significant.

Region pair	Stenohaline species		Euryhaline species	
	DD_4	Steinhaus' coefficient	DD_4	Steinhaus' coefficient
11–12	−0.2516	0.3169	NS	0.9399
12–51	−0.3176	0.6353	NS	0.8046
12–52	−0.3290	0.5160	NS	0.9372
21–22	NS	0.5733	−0.2914	0.6923
21–53	−0.3070	0.4166	NS	0.8108
21–54	−0.3320	0.5350	NS	0.9337
22–23	−0.3124	0.6508	0.2142	0.7173
22–32	−0.2715	0.4511	−0.2958	0.7376
22–53	−0.3053	0.4125	0.3381	0.5706
23–32	NS	0.6414	−0.3343	0.5654
23–53	−0.3313	0.6744	NS	0.7206
23–55	−0.3386	0.6415	0.3349	0.5686
31–32	0.3193	0.5565	NS	0.9212
31–42	−0.3298	0.4942	NS	0.7692
31–43	−0.2272	0.7338	0.3397	0.5353
31–55	0.2387	0.6823	0.2426	0.2929
31–60	−0.0494	0.7792	0.2782	0.3546
32–33	0.2295	0.2825	NS	0.9258
32–55	−0.2229	0.7089	0.2361	0.2826
41–42	−0.2488	0.7576	−0.3078	0.5010
41–58	0.2836	0.6517	NS	0.5926
41–60	0.3040	0.6760	NS	0.8058
42–43	0.3238	0.6452	0.3106	0.6421
42–60	0.3121	0.4961	0.2994	0.4337
51–53	−0.2275	0.8401	NS	0.7097
52–53	NS	0.8683	NS	0.7583
52–56	−0.2856	0.7736	NS	0.7971
53–54	0.2446	0.8217	NS	0.8651
53–55	NS	0.8998	NS	0.6870
53–59	−0.2237	0.8281	0.3338	0.5019
55–59	−0.1748	0.8360	NS	0.6591
55–60	−0.3028	0.7240	NS	0.7037
56–57	NS	0.8586	NS	0.9565
56–59	NS	0.8415	NS	0.6250
57–58	−0.1703	0.8704	NS	0.7143
57–59	NS	0.8090	NS	0.5882
58–60	NS	0.8293	NS	0.6857
59–60	−0.2131	0.8306	−0.3424	0.5625

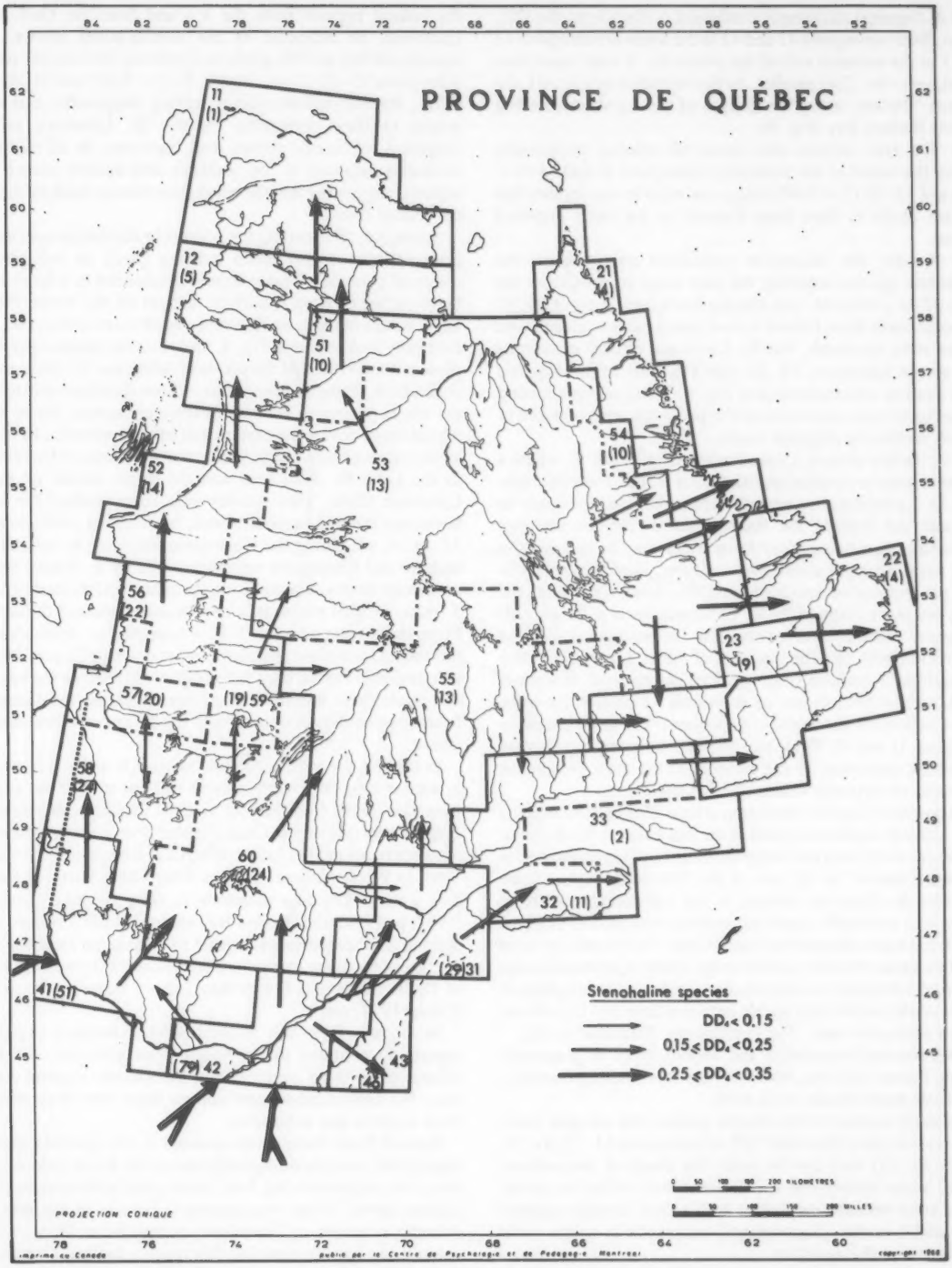


FIG. 5. Postglacial dispersal of the stenohaline species, as computed in this study. The arrows represent the direction and magnitude of the coefficient of dispersal direction (DD_4) for pairs of adjacent subregions. The numbers in parentheses, accompanying subregion identifications, are the numbers of species present in at least 25% of this region's pixels. The double-tailed arrows represent hypothesized incoming routes from inland (or sea: Fig. 7) glacial refugia.

(c) A dispersal movement northward is clear from the DD_4 arrows, from subregions 41 and 42 in the south to subregions 12 and 11 at the northern end of the peninsula. It must have been helped, up to the 52nd parallel, by the formation of glacial Lake Ojibway–Barlow, along the margin of the ice sheet receding towards Hudson Bay (Fig. 6).

(d) The DD_4 arrows also show the species progressing towards the centre of the peninsula, subregions 52 and 53 (S = 0.87) and 53–55 (S = 0.90) being so similar to one another that they are likely to have been formed by the same dispersal process.

(e) Finally, the dispersion coefficient arrows show the stenohaline species reaching the east coast regions from the centre of the peninsula, and coming down into rivers of the St. Lawrence north shore (which is now inaccessible to stenohaline species from the south, the St. Lawrence estuary containing sea water in subregions 33, 32, and 31). This whole dispersal process can be summarized as in Fig. 6. Mechanisms allowing the species to cross the centre of the peninsula are suggested in the next section on dispersal routes.

As for the low altitude areas of subregions 31 and 32, where a great similarity in stenohaline fish faunas is found on either side of the St. Lawrence, two complementary explanations may be proposed: (a) Toward the final stages of the ice melting, sufficiently large amounts of fresh water may have formed a partly unmixed layer above the sea water, near the shores, to allow the stenohaline species to progress down river along the shores and reach many of the St. Lawrence lower river and gulf tributaries. Such a layer exists now in the Saguenay Fjord (Drainville 1968). (b) The lowlands of the St. Lawrence Valley form a climatic gradient (Fig. 4), from colder (east) to warmer (west), so that both shores of subregion 32 present the same habitat, at least for the climatic component. The same is true for subregions 31 and 42. These two phenomena acting together are a possible explanation for the presence of the same stenohaline fish faunas on opposite shores of this seawater mass.

The number of species present in at least 25% of each region's pixels show an impoverishment of the fish fauna as the dispersal took place, northward and eastward (Fig. 5). This phenomenon can be accounted for by one of the following explanations: (1) either the dispersal process is not completed, and more species will eventually reach the northern and eastern regions, or (2) the species advance has been stopped by climatic or water condition limits that they cannot cross. Only experiments under controlled laboratory conditions, or experimental transplants in nature, could enable us to decide between these two hypotheses in each particular case. The correlations illustrated in Fig. 4 between regional boundaries and various types of potentially limiting factors indicate, however, that the limiting condition hypothesis must contain some truth.

The small number of stenohaline species that are now found in the seaside areas (less than 70% in subregions 11, 12, 21, 22, 31, 32, 33, 53) may also be partly the result of competition. Indeed, some stenohaline species may have failed to invade certain areas because euryhaline species had already occupied the available niches. Experimental transplants in nature could help to answer this question.

The map for the euryhaline species (Fig. 7) does not contain as many DD_4 arrows as Fig. 5 because the small number of euryhaline species present, often widely scattered, caused many arrows to be nonsignificant. The mechanism of entrance is here very different, since most euryhaline species must have reached the coastal regions from the sea and from the Gulf of St. Lawrence, as indicated by the double-tailed arrows. It is remarkable that no DD_4 arrow is significant between the pairs of subregions 33–32 (S = 0.93) 32–31 (S = 0.92) and 31–42 (S = 0.77), the euryhaline species having supposedly had equal access to these territories via the St. Lawrence estuary. Dispersal coefficient arrows lead, however, to all the inland territories adjacent to the southern and eastern coastal subregions, suggesting that the euryhaline species went up many of the coastal rivers.

Subregion 55 is among the poorest in euryhaline species, the dispersal arrows that reach it being partly an indication of dispersal potential. This potential is inhibited to a large extent by the series of steep waterfalls that cut off the lower from the upper basins of many St. Lawrence north shore rivers, shown by the heavy broken line in Fig. 4. Only two euryhaline species are present in 50–100% of the pixels of subregion 55: the ninespine stickleback, *Pungitius pungitius*, whose distribution extends to the whole peninsula, and the freshwater salmon, *Salmo salar*, whose range covers the eastern half of the peninsula, limited by a line running south roughly from the west coast of Ungava Bay to the Lake St. John area and the upper course of the St. Lawrence River. This species may have reached the inland territories through various routes: by rivers of subregions 22, 32, or 31, or, during the Champlain Sea episode (when Lakes Ontario and Champlain were colonized by *S. salar*), straight northward from subregion 31 to the centre and the east of region 5 (map: 51–60) where it is now found dispersed throughout. From there (according to V.L.'s hypothesis), descendants of this inland freshwater population went down to Ungava Bay as a new endemic searun population, now confined to the bay (i.e. not joining the regular Atlantic migrants on the Greenland feeding grounds), in accord with the three considerations that follow.

In the sea, the searun Atlantic salmon *S. salar* is not known to appear along the northernmost 100-km strip of the coast of Labrador (north from Ramah to Cape Chidley), nor along the Ungava Bay side of that Cape. Neither does it reach the extreme northern headland of Québec from Leaf River along the Hudson Strait to Wolstenholme, nor has it ever been found in Hudson Bay waters. The two mentions in Bergeron and Brousseau (1982, p. 49) for the Hudson Bay are freshwater *S. salar*. In our opinion, the searun seems unable to inhabit the local waters of Arctic origin, as appears to be also the case of the western waters of Davis Strait and Baffin Bay, where there are no salmon (Carter 1979, map).

In Ungava Bay, the Atlantic salmon forms a population apparently confined to the voluminous affluents of the bay tributaries, with no connection to the Atlantic migrant population. No Greenland-tagged salmon have ever been returned from Ungava Bay tributaries.

Salmon from these rivers possess a recognizable morphological trait, ecophysiologically tied to the Arctic climate of the area, i.e. scales showing 5–11 river years in the parr stage. No salmon above 7 river years appear to have been reported from Atlantic migrants in Greenland waters (Lear 1976). Consequently, we hypothesize that this species reached Ungava Bay through the inland routes described in the following section. Very peculiar behavioural traits, observed in 1979–81 on the Ungava Bay salmon population and recently reported by Robitaille et al. (1982), may support the idea that we are facing a new local searun population, born of a freshwater population.

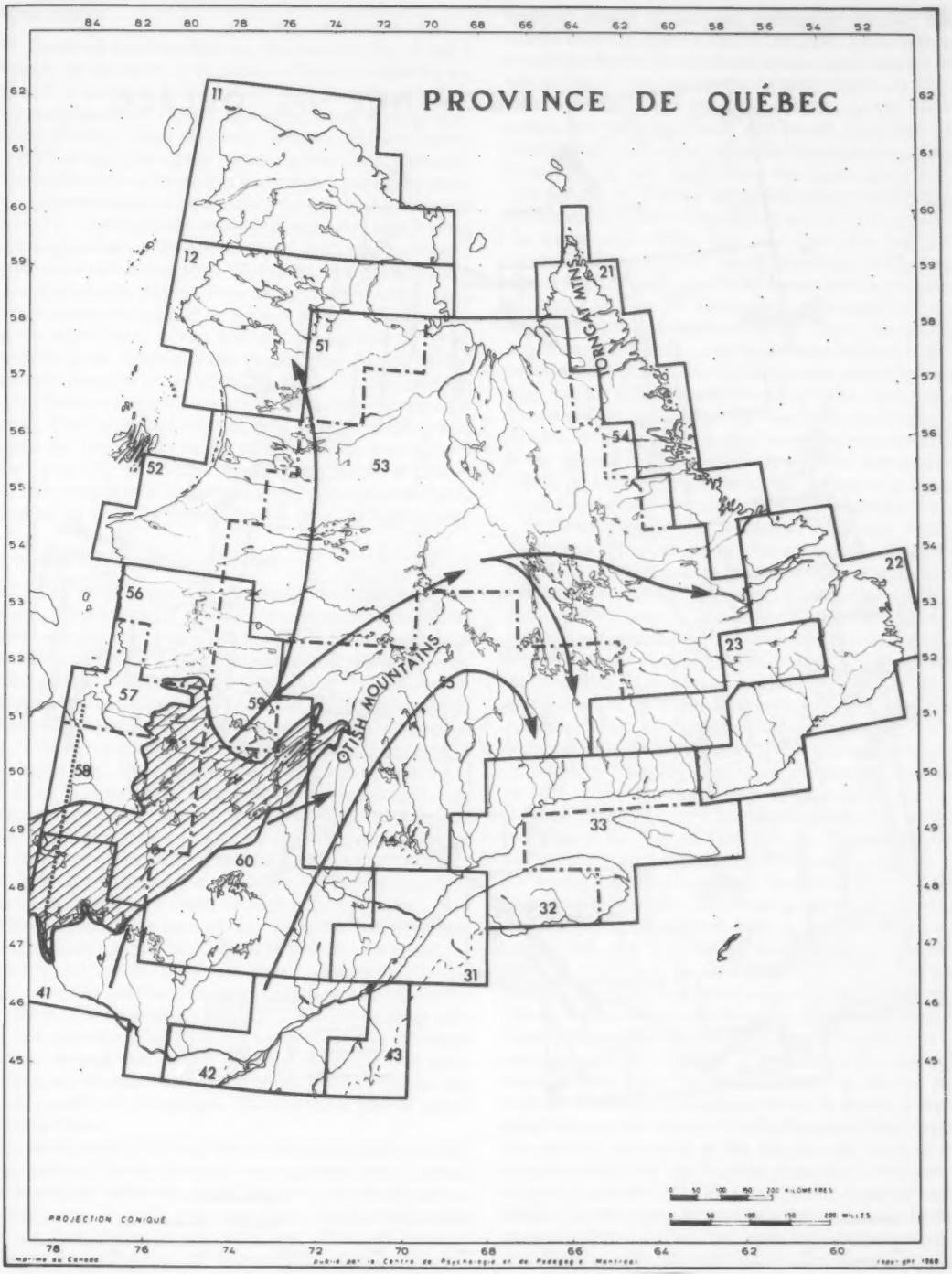


FIG. 6. Summary of the stenohaline species dispersal, detailed in Fig. 5. Hatched area: maximum extension of the Ojibway–Barlow glacial lake (Anonymous 1970).

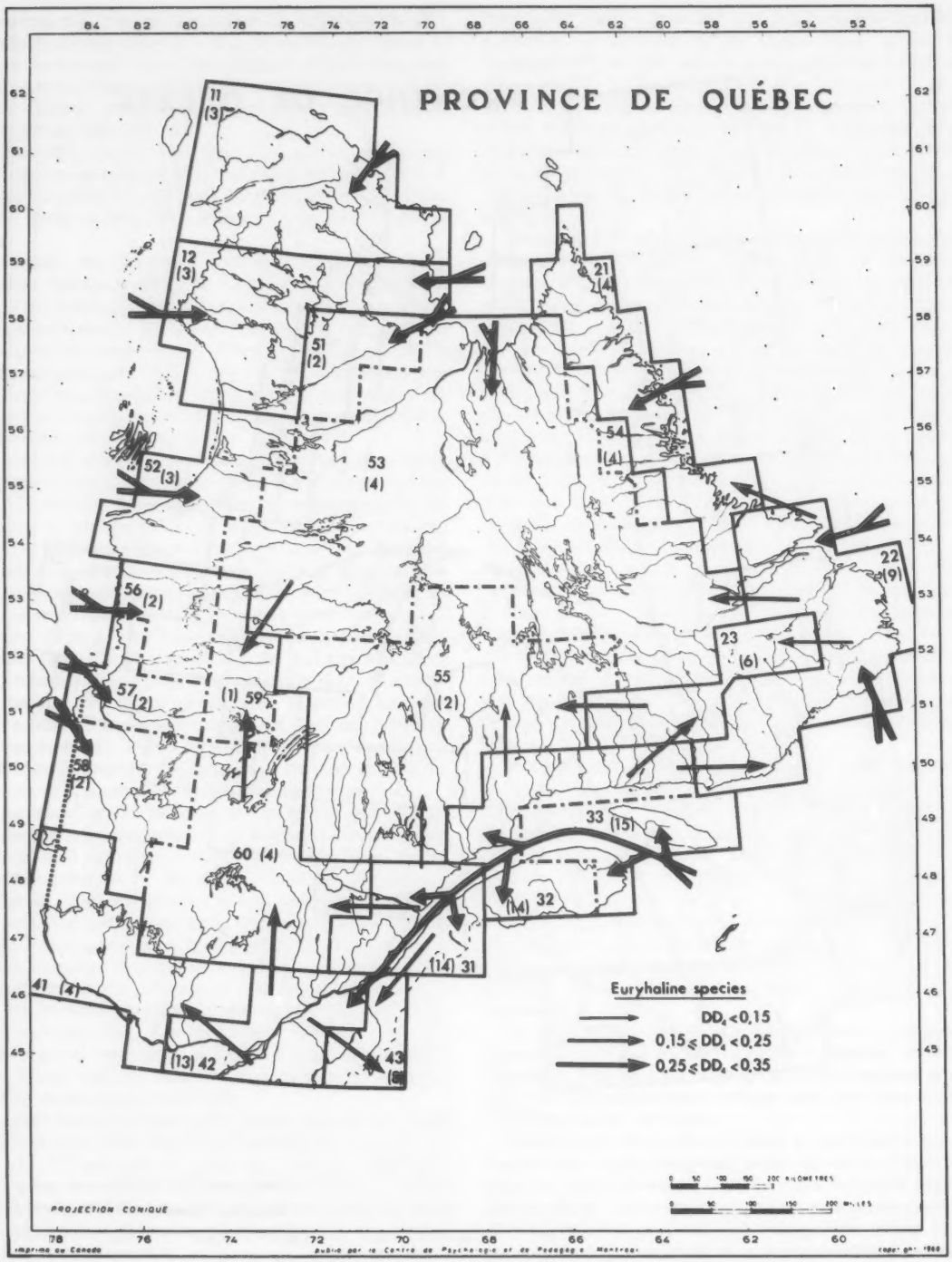


FIG. 7. Postglacial dispersal of the euryhaline species, as computed in this study. See Fig. 5 for details.

Dispersal Routes

The computed dispersal patterns illustrated in Fig. 5 and 7 presuppose the existence of physical mechanisms allowing the fish species to reach and cross the centre of the peninsula. Two non-mutually exclusive types of mechanisms can be suggested.

On the one hand, when the glacier disappeared from Québec about 6000 yr ago, the whole peninsula was tilted westward, with the northern tip of James Bay lower than at present by about 150 m, as shown on the isobase maps published by Andrews and Tyler (1977). Consequently, many river segments now flowing towards Ungava Bay or the Atlantic may have flowed westward, along the slope that existed then. We hypothesize that a dynamic process of gradually shifting river interconnections took place as the peninsula rose back to its present isobasic position.

On the other hand, a vast and unusual network of interconnections at the headwaters of the major rivers still exists, and radiates from the centre of the peninsula towards its edges (Fig. 8). These connections are mostly permanent but a few are seasonal. Their existence will not be a surprise to those who have had an opportunity to fly at low altitude over central Québec, since the area where the ice sheet melted is often a gigantic network of lake interconnections, a phenomenon that is not obvious on the blank map we used to draw the figures here.

Interconnected Rivers in the Americas

Watershed interconnections are known occasionally in the literature. The existence of Québec river connections is obvious in a few cases from the names of lakes on published maps, such as Summit Lake and lac à Deux Décharges, their waters flowing toward opposite watersheds. In other cases, indications are found in reports of the explorers of the last century. Many other connections were found by a careful examination of topographic maps, followed by checks on aerial photographs or, in doubtful cases, in the field. Direct evidence of river interconnections in the Gulf of St. Lawrence North Shore area was also obtained through correspondence with M. Jean-Marie Brassard (Research Service of the Ministère du Loisir, de la Chasse et de la Pêche du Québec), who was interested in the question and "had been there" himself by canoe. Our quest for river interconnections began as the result of a chain of haphazard encounters with published reports. Our interest was triggered because interconnected rivers, on the one hand, are relatively rare aspects in geography and, on the other, are utterly unsuspected by the public, except for scattered regional specialists who may know about them. For example, a university lecturer in geography said a few years ago to his class that a lake could only discharge its waters through one outlet. This flat statement was quite credible to his students, since liquid water in natural masses has essentially one level, not several. This simplistic view of nature must be rectified.

Only about half of the citations on interconnected rivers that we encountered in the literature are reported here. Natural interconnections only are considered, to the exclusion of man-made ones. We will now try to show that interconnected rivers are rare events in the Americas. This will help to emphasize the exceptional configuration found in the Québec peninsula, which is the basis for one of the two mechanisms suggested above to explain the crossing of the centre of the peninsula by stenohaline fish species.

In the Rocky Mountains of the United States, along the continental divide, there is the Two-Ocean Pass in Wyoming, where each of at least two streams forks on the near-level, alpine meadow ground of the pass, outflowing branches from each reunite from the opposite ends of the pass. These branches flow toward the Pacific Ocean via the Snake and Columbia rivers, on the one hand, and toward the Atlantic Ocean via the Yellowstone, Missouri, and Mississippi rivers, on the other. "It is certain that there has been, and usually is, a free waterway through Two-Ocean Pass of such a character as to permit fishes to pass easily and readily from the Snake River over to the Yellowstone — or in the opposite direction," said ichthyologist Evermann (1893) after visiting the area on 17 August 1891. For the eastern side of the continent, the same author recalled another author's citation, "in the highlands of Maine, where a rivulet discharges a portion of its waters into the Atlantic and the remainder into the St. Lawrence"; unfortunately, we did not succeed in retracing this on our maps. Then, "Two-ocean Pond in Yellowstone Park.... During the flood seasons, it discharges on the eastern rim into the Gulf of Mexico, and from the western edge into the Pacific ocean" (Redway 1890). In the same way, Talcott (1894) reported on Portage Lake, discharging both in Rivière du Loup in Québec, and in the north and south branches of the West Branch of Penobscot River in Maine. Thompson (1842, Part III, p. 67) reported on a pond with two outlets, located in northern Vermont, south of the Québec border.

In South America, in southern Venezuela, Territorio de Amazonas, the upper Orinoco River suddenly divides into two branches. Its main stream continues flowing west, then north and northeast toward its gigantic delta on the Atlantic Ocean south of the Island of Trinidad, while a large branch turning abruptly southward, the Casiquiare River, connects via the Rio Negro with the Amazon River in Brazil to flow toward the Atlantic. This interconnection of two great streams, perhaps the first known of its kind, appeared on a 1738 map by Father Antonio Caulin, in a geographical description of the Orinoco watershed (Caulin 1779 (1958), p. 296). To satisfy his curiosity, Alfred Russel Wallace went to see the place of the connection in 1851, also providing a map of these rivers, and he rather unkindly stated that, 50 yr before, Alexander Humboldt had not reached that far (Wallace 1889 (1972)). The diverging branches are indicated by arrows in the *National Geographic Atlas of the World* (National Geographic Society 1970, p. 74, 76). This explains directly how these two great streams, so far apart according to usual notions, have in part the same fish fauna, such as the great "electric eel" *Electrophorus electricus* (Berg 1947, p. 444). As at the Two-Ocean Pass in the United States, there is, according to a recent map of Ecuador, and sitting also just on the continental divide in the Andes 40 km directly east from Quito, a lake with two discharges. One flows west, finally joining the Rio Esmeraldas, a tributary of the Pacific Ocean, while the other, flowing east, connects via the Río Marañón with the Amazon (Anonymous 1974). In Brazil, a connection exists between the Amazon (via the Tocantins River discharging near Belém, just south of the equator and south of the vast Amazon delta) and the Rio San Francisco, a tributary of the Atlantic, at about 10°15′S, some 300 km south of the city of Recife. The two rivers have at least three species of Cichlidae in common (Haseman 1912, two maps tracing stream connections, also rejecting some other previously cited connections for South America).

Several examples exist in Canada. In northern Saskatchewan, Lake Wollaston has two northern outlets (National Geographic Society 1970, p. 56, 63), one leading west toward Lake Athabasca, flowing to the Mackenzie River (a tributary of the Arctic Ocean, at the western end of Mackenzie District in the

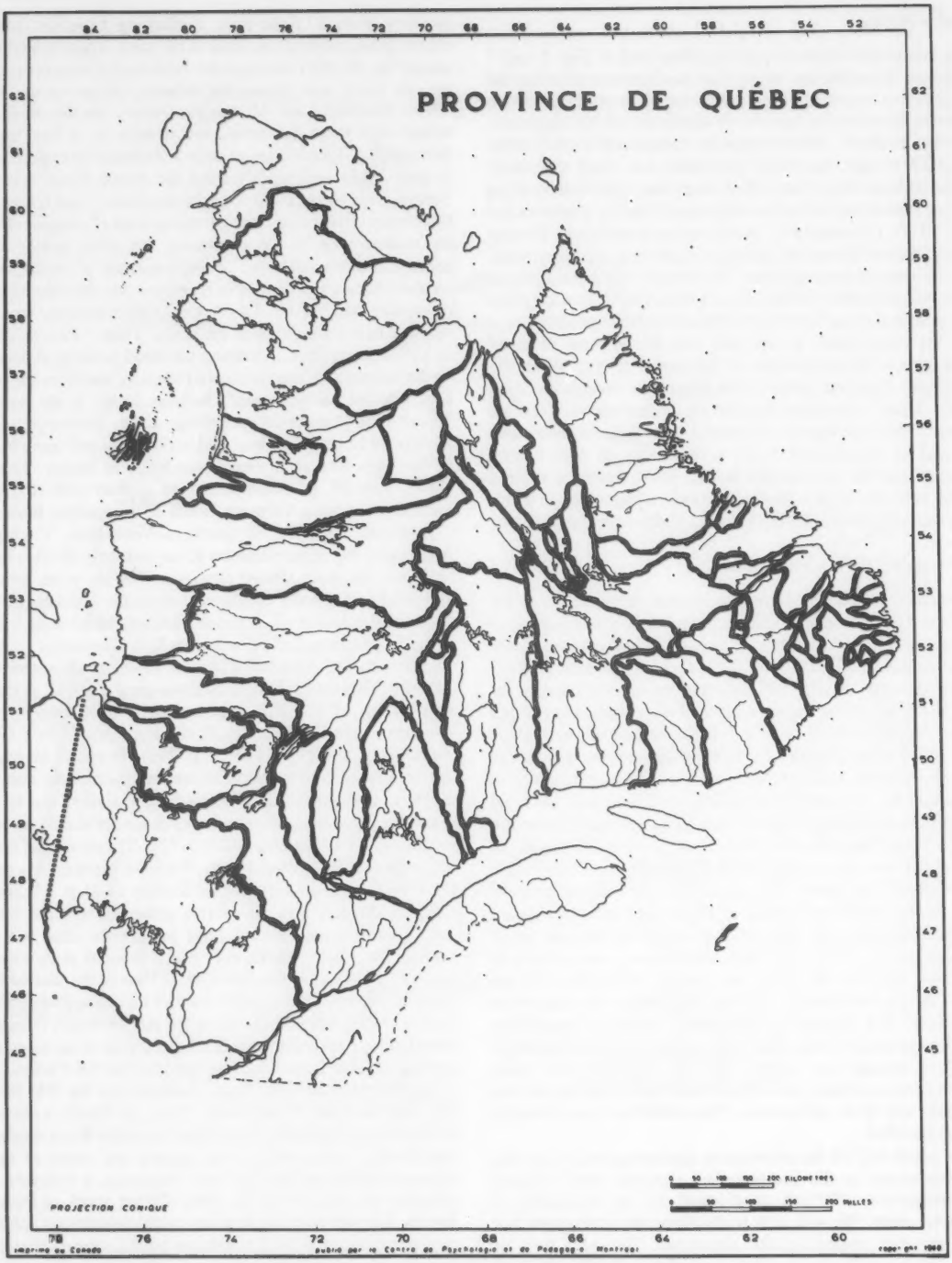


FIG. 8. Present network of river interconnections in the Québec peninsula.

Northwest Territories), and the other outlet flowing east and then south to the Churchill River, a tributary of Hudson Bay, on its west coast in northeastern Manitoba. E. A. Preble explained the presence of the grayling *Thymallus arcticus* in the lower Churchill River, tributary to Hudson Bay, by a direct water connection with Athabasca Lake (cited in Chambers 1914, p. 296). In the Canadian Rocky Mountains, at the Athabasca Pass, a small two-outlet lake sitting again on the continental divide was discovered 17 October 1824 by the Hudson's Bay Company governor, George Simpson (cited in MacKay 1966, p. 186–189). It discharges east into the Athabasca River and west into the Columbia River. The latter historian added: "Today the line separating British Columbia from Alberta divides this tiny lake." The lake is found as described on two old maps (Sproat 1873; Anonymous 1900); in Anonymous (1900, p. 6), the lake name is the one given by Simpson: Committee's Punch Bowl. As a consequence, Lake Athabasca, in northern Alberta and Saskatchewan, has a present-day continuous connection with four watersheds outflowing at near right angle directions: one direction south and west, to the Pacific Ocean, via the Athabasca and Columbia rivers; another one south, to the Gulf of Mexico via the Two-Ocean Pass and Columbia River connection with the Mississippi; another north, to the Arctic Ocean via the Mackenzie River; and the last one east, to Hudson Bay via the Churchill River. Thus, common fish species, or sister species, eventually evolved within these watersheds after the deglaciation, such as seen today among the Coregoninae (*Prosopium cylindraceum* and *P. williamsoni*) and the Catostomidae (*Catostomus commersoni* and *C. macrocheilus*), may become readily explained distributional patterns. Finally, there may be yet another two-ocean connection in the Canadian Rockies, in the vicinity of Kicking Horse Pass. Along highway 93 in Alberta, between Banff and Jasper, there is a stream that forks into two branches. One of them reportedly ends up in the Atlantic and the other in the Pacific. This was related to us by Jeanne and Thérèse Legendre, sisters of the second author, who heard it in 1977 from a Brewster Company bus driver and tourist guide.

In central Ontario, the Muskoka River offers two peculiarities (Canadian federal maps 31D, 31E and 41H, scale 1:250 000). First, about 5 km west of Lake Muskoka, this river bifurcates, both branches (Moon and Muskoka) flowing toward Georgian Bay. Farther downstream, the Muskoka River flows into Go Home Lake, which has two outlets (Go Home and Muskoka), both flowing again toward Georgian Bay (P. Ross, Université de Montréal, pers. comm.). Since all three courses flow toward Georgian Bay (Lake Huron), this hydrological curiosity would not be expected to have much impact on fish distributions. Such is not the case with a lake, located on the heights of the Laurentide Peneplain in eastern Ontario: Lake Timagami connects through a maze of lakes and rivers, as shown on maps, north and then east with Lake Témiscamingue located between the provinces of Ontario and Québec, a headwater of the Ottawa River (which is a large tributary of the St. Lawrence). Lake Timagami also connects to the south with Lake Nipissing, which flows to Lake Huron via Rivière des Français (Canadian federal maps, scale 1:250 000, here given in a succession so as to follow the course of the waters: 31M, 41P, 41I, 31L; maps not repeated in the References). On map 41P/1, scale 1:50 000, the northern connection of Lake Timagami with the Ottawa River is found just south of the line between Canton Township in Nipissing District to the south and Medina Township in Timiskaming District to the north. Confirmation of this geographical water arrangement is found in the literature (Chénier 1937, p. 51).

On the Atlantic side of Canada, "from some marshy lakes on the isthmus which connects Nova Scotia with the mainland the river Missiquash flows to the Bay of Fundy; a small stream, sometimes dry in summer, also flows northward from the same lake to the Baie Verte [on the Gulf of St. Lawrence side of the isthmus]" (G. 1891). This hydrologic situation may explain how some of the smaller fish species, more or less indifferent to water salinities, are found on either side of the isthmus. They may have often crossed it directly from the Atlantic – Bay of Fundy side to the Gulf of St. Lawrence side. The distributional maps of some of these species found to occupy waters of the isthmus (Livingstone 1953) suggest that such crossover fish species may be those, for example, of the families Petromyzontidae (*Petromyzon marinus*), Clupeidae (*Alosa pseudoharengus*), Salmonidae (*Salvelinus fontinalis*), Osmeridae (*Osmerus mordax*), Anguillidae (*Anguilla rostrata*), Cyprinodontidae (*Fundulus diaphanus* and perhaps *F. heteroclitus*), Gadidae (*Microgadus tomcod*), Percichthyidae (*Morone americana*, and perhaps also *M. saxatilis*), and Gasterosteidae (all three so-called marine species, *Apeltes quadracus*, *Gasterosteus aculeatus*, *Pungitius pungitius*).

Freshets and their effect on fish migrations are a universally ignored mechanism. This may be tied to their year-to-year variability and to their usually short duration. During these brief periods, however, the volumes of water exchanged between watersheds are often considerable, so much so that large communities of fishes may be passively transported. Under northern North American climatic conditions, freshets may occur at any time of the year, for example, during autumn rains and spring heavy snow thaws, and after heavy local summer rainfalls. Even though occasional, their erratic recurrence during decades or centuries has undoubtedly acted in the past as an efficient intermediary (in time) mechanism in passive migration or transportation of fishes. Ichthyogeographers seem to have forgotten them. Such temporary interconnections between watersheds were heavily cited in the past throughout North America; some examples follow. First, there was the case of repeated seasonal "modern" (i.e. postglacial) connections between southern Lake Michigan and the Mississippi River, as related by the second discoverer of the Mississippi, La Salle (1682 (1879), p. 166). Weld (1807, Vol. I, p. 69, 330) documented a seasonal, northern Green Bay connection with the Mississippi. In northwestern New York, Wright (1918, p. 544) mentioned a connection between the Susquehanna River and Lake Ontario via Lake Cayuga, among the Finger Lakes. In northwestern Canada, as elsewhere, a river that normally functions as a lake outlet will not reverse and flow into the lake. There is, however, the exception of a river playing both roles alternatively according to whether it is in the freshet season or in some other time of the year. This occurs because of a local converging set of geographical conditions at the west end of Lake Athabasca. Two large rivers converge, the Athabasca from the south and the Peace from the west, with a rather large lake, Lake Clair, acting as a stabilizer between them in much the same way as do stabilizing basins erected alongside man-made canals for navigation. On 22 September 1808, a fur trader with the Northwest Company wrote: "...with a number of persons, in several canoes, I left Fort Chippewyan [at the west end of Lake Athabasca]; and, after coming two miles in Athabaska Lake, we entered a small river [small in terms of the country], which is about thirty six miles long [one of several local outlets of the big

lake], and which now [in September] runs out of that Lake into Peace river; but, when this river [the small one] is high, it discharges itself into the Lake [Athabasca]" (Harmon 1911, p. 140). Concerning streams that flow into the St. Lawrence, from its Québec north shore, an early nineteenth century army engineer had this to say after an exploration party set out to open the country to colonization: "These lakes discharge themselves by innumerable shallow streams, into the St. Maurice [tributary of the St. Lawrence just below Lake St. Pierre, or St. Peter] and aux Lievres [tributary of the Ottawa River] Rivers...; in one or two instances the streams swell into large and rapid rivers and discharge [westward] into the Ottawa and [eastward] Lake St. Peter in a direct course" (Ingall 1831, p. 14). At the beginning of the present century, several large parties supported by business and the Québec government explored the territory for extensions of railways to James Bay, and one of their land surveyors wrote: "The Height of Land between the St. Lawrence and James Bay waters is scarcely perceptible, the waters interlock and some of the lakes discharge both ways during freshets" (O'Sullivan 1903, p. 23). An accompanying map showed the permanent connection between the headwaters of the St. Maurice River (the previously cited tributary to the St. Lawrence) and Nottaway River, tributary to the southeastern end of James Bay, following precisely the same line as the southeast–northwest one shown at the extreme lefthand side of Fig. 8. The interconnection is a two-discharge lake, shown on present-day maps.

In Québec, such direct interconnections between rivers were never mentioned in the approximately 500 accounts of travels and explorations since the discovery of the country by Europeans, written by, or for, coureurs de bois, voyageurs, furriers, missionaries, businessmen, and soldiers. Such mentions appear only after the first quarter of the last century with the advent of naturalists attached to exploration parties, sent out to establish the possibilities of opening the then backcountry to colonization. To our knowledge acquired from these readings, the first documented connection, found in 1828, is the well-known three-discharge Lake Kénogami (Baddeley 1829, p. 117; Ballantyne 1851, map), 3 km wide on the average, 27 km long, and 102 m deep. This glacially formed fjord, about 15 km south of and parallel to the upper Saguenay River, has one natural outlet (la Belle-Rivière) westward to Lake St. Jean (St. John), and two parallel eastern outlets, Rivière des Sables and Rivière Chicoutimi, flowing northward toward the Saguenay River. Another Québec river interconnection was reported in 1859 by Ferland (1859, p. 111) between River St. Augustin, a North Shore tributary of the lower Gulf of St. Lawrence, and Kenamou River which falls into Baie des Esquimaux (Hamilton Inlet).

The Québec exploratory reports of the Canadian geologist A. P. Low were the initial incentive to our inventory when V. L. came upon them some 30 yr ago. Low criss-crossed the land from Hudson Bay to the Atlantic and from Ungava Bay to the St. Lawrence, toward the end of the last century. He wrote about Summit Lake, which has two outlets, one going to Ungava Bay via the Kaniapiskau and Koksoak rivers, and the southern one being a tributary of Manicouagan River that empties into the Gulf of St. Lawrence. He added: "This is not an uncommon case with lakes situated along the watershed in the northern region underlain by Laurentian rocks....Lake Kaniapiskau has *three* discharges" (our italics) (Low 1897, p. 107L). The following citation, with bracketed references, shows that tracing back old geographical autochtonous names of maps would be in itself quite a story if detailed: "The Great Whale river...is divided [upstream] into two almost equal branches...the Abchigamich [then the Indian name of the presently named Great Whale River, later extended to its course above the fork] and Coast branches of the river....This stream [the Abchigamich], according to the Indians [Low was not there himself to check], takes its rise in a large lake of the same name [now called Lake Bienville, 110 km long east–west] situated about 100 miles [160 km] farther inland. A striking peculiarity of this lake is that it has *several* outlets and being situated directly on the height of land, it drains eastward by a tributary of the Koksoak river which empties into Ungava bay, while its westward flowing outlets form the head waters of the Abchigamich [Great Whale] river and also of the Little Whale river [both tributaries to the eastern shore of Hudson Bay]. Such lakes with *double* outlets are not uncommon in Labrador, but it rarely happens that *three* rivers take their rise in the same lake" (our italics) (Low 1903, p. 35D–37D). In former atlases, Lake Bienville had its Indian name corrupted otherwise, such as "Apickacumish" (Walling 1875, maps p. 15, 99, 103) and "Apiskigamish" (Rand McNally & Company 1938, map p. 17). There is a correction to make in Low's last citation. It seems he probably misunderstood his Indian counsels, as he gives Lake Bienville (Abchigamich) as a tributary of Koksoak River, which it is not. There is in fact a continuous connection between them, but it is through a set of four lakes (Lenouiller, Novereau, Decoigne, and Jacquemont) all at the same altitude and higher by some 30 m than both Lake Bienville and the Koksoak River (map 23M). It is these small lakes that discharge toward either watershed and that are thus the headwaters. On the other hand, we never succeeded in finding a connection between Lake Bienville and the Little Whale River, so that it looks as if there are only two present-day interconnections with Lake Bienville, i.e. that of the Great Whale and that of the Koksoak. Another hypothesis may be formulated, however: the Little Whale River connection with Lake Bienville may have been extant when Low talked with the Indians, and it may have drained out since then, due to the action of one or several occurrences such as (1) the considerable isostatic rebound of the Hudson Bay side of Québec, which may have broken the water connection (140 m rebound in the past 6000 yr, according to Andrews and Tyler (1977, fig. 6), i.e. about 230 cm/100 yr), (2) a possible filling up of headwater lakes by aquatic plants, turning the water bodies into more or less dried-up bogs, and (3) the less abundant rainfalls since the end of the "Little Ice Age," which started in the fifteenth century and terminated around 1890. If this hypothesis is correct, it would make it a case of a connection disappearing in historical times.

One way or the other, it was Low's provocative words, "three discharges," "two outlets," "this is not an uncommon case," etc., that launched 10 yr ago our overall examination of the Québec maps available, with the purpose of possibly locating other multiple-outlet lakes that he had not named or otherwise indicated. The result is Fig. 8. At the present state of our research, and apart from the freshwater part of the main St. Lawrence River, 41 rivers are seen to be interconnected today via 68 headwaters. This is a hitherto unheard of (if not intolerable!) situation. To cite only a few examples of explanations of the present distribution of some freshwater fish species, this incomparable, extensive, and multiple-connection network of rivers may be considered as a simple mechanism explaining how fishes, starting from Upper St. Lawrence waters, came, through centuries or millenia, across the Québec penin-

sula and reached eastward to the Hamilton Inlet (*Catostomus catostomus, C. commersoni, Rhinichthys cataractae, Couesius plumbeus, Lota lota*; Backus 1957) and to the lower reaches of the southern tributaries of Ungava Bay (Bergeron and Brousseau 1981), and even to the very northern extremity of the mainland close to Hudson Strait (*Salvelinus namaycush, Esox lucius, C. catostomus*; Bergeron and Brousseau 1981).

To our knowledge from the literature, there is no other reported instance of connections as extensive as the network discovered and described here. By analogy with the blood capillary networks of anatomy, we call it the *rete mirabile* (admirable network) of Québec rivers.

The postglacial dispersal patterns of fishes in the Québec peninsula can then be explained on the one hand by the isobasic movements of the peninsula since the end of the Wisconsin Ice Age, and on the other by the very elaborate network of river interconnections still extant today. In this way, dispersal routes were available for most fish species to reach all parts of the peninsula.

Acknowledgments

We are indebted to Prof. G. F. Estabrook, University of Michigan (Ann Arbor), who suggested the counter-examples to assumption (2.2), discussed under Materials and Methods, and to Dr. L. P. Lefkovitch, Agriculture Canada, who suggested the way of testing the symmetry of the binary form of the coefficient of dispersal direction. M. Alain Vaudor, computer analyst in the Département de Sciences biologiques, Université de Montréal, produced a manageable computer program for clustering with spatial constraint. This program is written in PASCAL for a CDC/CYBER computer and, although cut to fit the shape of our study region and our type of data input, could be made available to other workers for fundamental research purposes. We acknowledge the work of M. Vincent Jarry who took care of the input of the 109 species data maps into the computer. Thanks are also due to Dr. Philippe Ross for his critical review of the manuscript. Many thanks are due to Dr. L. J. O'Brien, Director General, Surveys and Mapping Branch, Energy, Mines, and Resources Canada (Ottawa), for providing us so willingly, through correspondence, with several stereoscopic aerial photos of upland Québec areas, which were invaluable in deciding watershed interconnections. Our deepest appreciation goes to the personnel of the Ministère du Loisir, de la Chasse et de la Pêche, Gouvernement du Québec, for their sustained and enthusiastic support of this research: Mm. André Laforte, Directeur Général, Région de Montréal, and Bernard Vincent, Chef du Service de l'Aménagement et de l'Exploitation de la Faune, for their logistic contribution to this work. We are also grateful for the help provided by members of their staff: M. Richard Mathieu, Librarian, and Mlle Jacqueline Carbonneau, Library Technician, for loans, acquisitions, and many interlibrary loans of documents, and M. Gilles Roy for his continued and careful attempts at locating river interconnections on topographic maps. Also, to M. Jean-Marie Brassard, biologist, for providing us with new river interconnections and confirmation of others. Finally, to M. Roger LeJeune, biologist, for his unfailing support in the realization of this work. This research was supported by grants from the Natural Sciences and Engineering Research Council of Canada (No. A7738) and from the Ministère de l'Education du Québec (No. EQ-0467). Computing time was provided by the Centre de Calcul, Université de Montréal.

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Influence of Reservoir Transit on Riverine Algal Transport and Abundance[1]

D. M. Søballe[2] and R. W. Bachmann

Department of Animal Ecology, Iowa State University, Ames, IA 50011, USA

Søballe, D. M., and R. W. Bachmann. 1984. Influence of reservoir transit on riverine algal transport and abundance. Can. J. Fish. Aquat. Sci. 41: 1803–1813.

The Des Moines River lost 65–75% of its algal standing crop (chlorophyll *a*) in passing through each of two impoundments (mean retention times 11 and 16 d), and chlorophyll concentrations within both impoundments were 50–90% below the predictions of empirical chlorophyll–nutrient models. Sedimentation of river-borne algae and light limitation within the impoundments were identified as major loss processes. A reduction in algal size from upstream to downstream in one reservoir paralleled the loss of algal biomass. Algal losses in each impoundment increased with both increasing retention time and water temperature so that chlorophyll concentration below the dams was uncoupled from the temperature and flow dependence seen in river reaches not influenced by impoundments. The reduction in riverine algal transport associated with reservoir transit was cumulative over the two-reservoir series; this reduction can be interpreted as a "reset" to river headwater conditions.

Nous avons constaté que lors de leur passage dans deux bassins de retenue (séjour de 11 et 16 jours en moyenne), les eaux de la rivière Des Moines ont perdu de 65 à 75 % des algues (chlorophylle a) qu'elles contenaient ; la concentration de chlorophylle dans chacun des deux bassins était de 50 à 90 % inférieure à la valeur prévue suivant des modèles empiriques représentant la teneur en chlorophylle et en éléments nutritifs. Ce phénomène est principalement dû au fait que la lumière est réduite dans les bassins et que les algues transportées dans les eaux de la rivière se déposent. Parallèlement à cette baisse de biomasse, nous avons observé dans l'un des bassins que la taille des algues diminue d'amont en aval. La quantité d'algues qui disparaissent des eaux dans chaque bassin augmente suivant la longueur du séjour et la température de l'eau, si bien que la concentration de chlorophylle en aval des barrages ne concorde pas avec la température et le courant observés dans les parties de la rivière où les effets du séjour en bassin de retenue ne se font pas sentir. La disparition des algues durant le séjour en bassin de retenue est cumulative ; on peut considérer que les eaux retournent à l'état où elles étaient à la source.

Received November 9, 1983
Accepted September 6, 1984
(J7604)

Reçu le 9 novembre 1983
Accepté le 6 septembre 1984

Lakes and impoundments trap dead and inorganic material carried into them from their catchments, but the fate of living organisms carried into a lake or impoundment has received less attention, probably because many low-order streams flowing into lakes do not have a significant plankton. Large rivers, however, often carry a concentrated suspended biota (Hynes 1970) and these rivers are increasingly subjected to impoundment. The streams of central Iowa transport high concentrations of suspended algae, particularly diatoms (Swanson and Bachmann 1976), and impoundment of these rivers should have a noticeable impact on the riverine algal assemblage.

River–reservoir systems are characterized by transitions between riverine and lacustrine conditions (Thornton et al. 1980). The change to lacustrine conditions tends to eliminate those river-borne algae that are ill-suited to a lentic habitat (e.g. Brook and Rzóska 1954; Round 1981), whereas the return to riverine conditions below the dam removes those reservoir-produced algae that are not suited to riverine conditions (reviewed by Hynes 1970). The observed pattern of algal abundance in river–reservoir systems should thus depend upon the source, concentration, and environmental requirements of the transported algae and upon the duration and intensity of changes in abiotic variables, such as turbulence, light, and nutrient availability, associated with river–reservoir transition zones.

Changes in algal abundance associated with transit through reservoirs will alter riverine patterns of algal transport downstream. Ward and Stanford (1983), in their "serial discontinuity concept," and Vannote et al. (1980), in their "river continuum concept," contended that river transport patterns change predictably from upstream to downstream. They speculated that reservoirs may "reset" this longitudinal trend so that sites below an impoundment may show transport characteristics normally expected farther upstream or downstream. In these models the reset is largely determined by reservoir location within the river system. The models do not address the role of in-reservoir processes or process variability. Both Vannote et al. (1980) and Ward and Stanford (1983) noted the absence of data (particularly from nonforested watersheds) needed to test their concepts.

[1]Journal paper No. J-11229 of the Iowa Agriculture and Home Economics Experiment Station, Ames, IA, Project 2483; publication No. 2415 of the Environmental Sciences Division, Oak Ridge National Laboratory, Oak Ridge, TN.

[2]Present address: Environmental Sciences Division, Oak Ridge National Laboratory, Oak Ridge, TN 37831, USA.

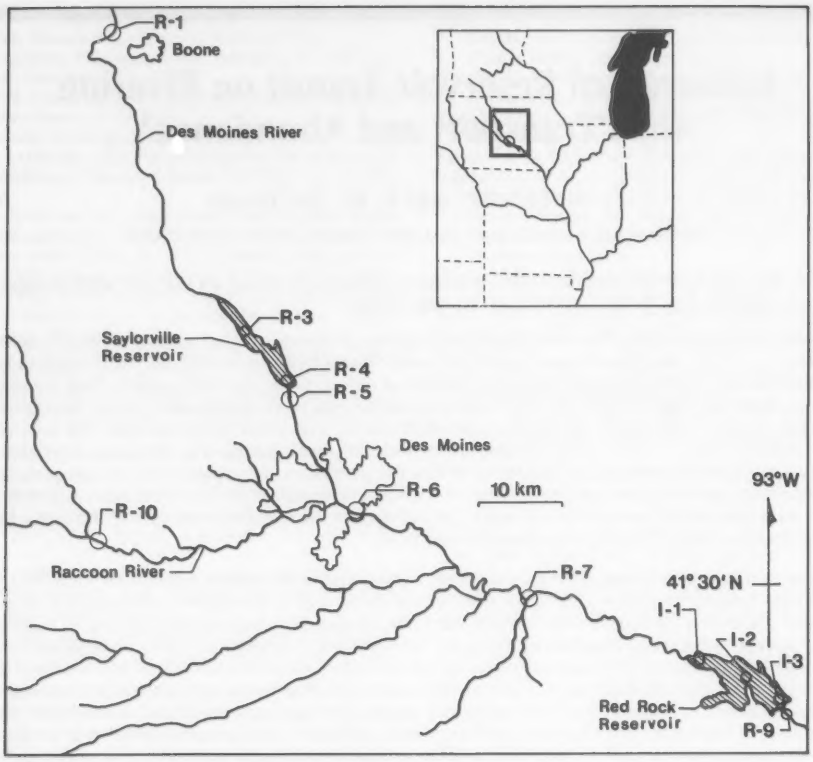

FIG. 1. Location of sampling sites. Inset shows location of study area in relation to Central United States.

Algal transport and abundance in unimpounded Iowa rivers are dominated by physical processes (Swanson and Bachmann 1976) and show a distinct upstream to downstream trend. Because Iowa has some of the highest surface water concentrations of phosphorus and nitrogen in the United States (Omernik 1977), Kilkus et al. (1975) concluded that plant nutrients were unlikely to be major factors limiting algal densities in these streams. Instead, they found that algal chlorophyll concentrations and cell counts in a given stream were directly related to water temperature and inversely related to flow volume.

Swanson and Bachmann (1976) developed a model for Iowa streams to explain the observation that average algal exports (algal concentration times flow volume) among streams or among different stations along the same stream increase with the area of wetted streambed upstream from the sampling point. They hypothesized that algae drifting in Iowa streams are derived primarily from benthic populations. In their model, increases in flow volume at any given point dilute a relatively constant contribution from the streambed, and this explains the observed inverse relationship between concentration and flow.

The Des Moines River is the major river of central Iowa and drains an unforested prairie devoted to intensive row-crop agriculture. The river is generally turbid, with high concentrations of inorganic nutrients and suspended solids. Dense algal crops (i.e. chlorophyll $a > 400$ mg/m^3) have been frequently observed in the water column (Kilkus et al. 1975; Burkholder-Crecco and Bachmann 1979) and euplanktonic diatoms (*Stephanodiscus, Cyclotella, Melosira, Asterionella, Fragilaria*) usually dominate this assemblage (Drum 1981; Kilkus et al. 1975).

Recently, two major impoundments were constructed in series on this river, giving us the opportunity to examine the effects of these reservoirs upon riverine algal transport and abundance and to study within-reservoir processes that produce these effects.

Methods

Study Area and Field Monitoring

Two major impoundments are arranged in series on the Des Moines River (Fig. 1). Saylorville Reservoir (impounded in 1978) has a 15 100 km^2 drainage and is located directly upstream from the city of Des Moines. This impoundment has a 2200-ha surface area (at normal pool elevation) and a mean depth of 4.1 m. Average hydraulic retention time during this study was about 16 d. Red Rock Reservoir (impounded in 1969) is located 65 km downstream from the Saylorville dam and is directly below the city of Des Moines. It has a drainage area of 32 000 km^2, or 17 000 km^2 if the area above Saylorville dam is excluded. At normal pool elevation the reservoir surface area is 5400 ha and the mean depth is 2.2 m. The average hydraulic retention time in Red Rock Reservoir during this study was 11 d.

Several low-head (1–3 m crest) dams are on the main stem of the Des Moines River above station R-1, and numerous lakes and small impoundments are located in the river headwaters

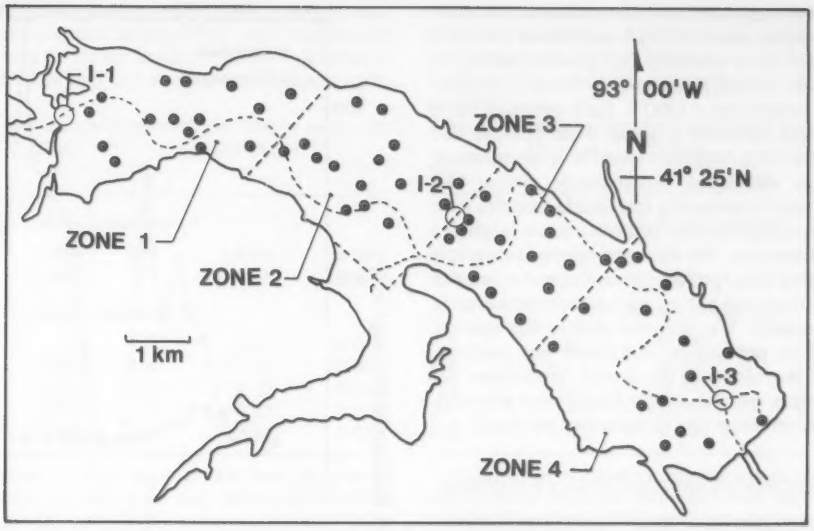

FIG. 2. Sediment (solid circles) and water column (open circles) sampling sites at Red Rock Reservoir. Longitudinal sediment zones and old river channel are delineated with broken line.

(150–200 km above station R-1). The Raccoon River has no impoundments on its main stem, but ponds and small dams can be found within its drainage.

Samples were collected weekly from eight sites in the Des Moines River and Saylorville Reservoir (Fig. 1) between 6 November 1979 and 28 October 1980 (only the ice-free period, from April to October, is considered here). Weekly physical–chemical sampling and in situ primary productivity measurements (light–dark bottle, dissolved oxygen method) were conducted between 27 June 1979 and 30 September 1980 at three mainstream sites in Red Rock Reservoir (Fig. 2). Water samples for chemical analysis were collected with a Van Dorn type sampler and were stored on ice and in darkness until returned to the laboratory for analyses by standard methods (APHA et al. 1975). Full details of Red Rock Reservoir sampling methods, dates, and analytical procedures appear in Søballe (1981).

Red Rock Reservoir Algal Biomass Budget

We constructed an algal biomass (chlorophyll *a*) budget to synthesize quantitatively the physical–chemical and productivity data. Red Rock Reservoir was divided into two segments and the surface area of each was estimated planimetrically. Soundings from a sediment study (discussed later) gave average depth information. Algal transport past three reservoir sampling stations (I-1, I-2, I-3, Fig. 1) was calculated for each sample date by multiplying chlorophyll *a* concentrations by reservoir inflow. This assumes that flow through the reservoir is unidirectional and conservative.

We estimated in situ inputs of organic carbon from primary productivity data. Oxygen evolution was divided by a photosynthetic quotient of 1.2 (Strickland and Parsons 1968) to convert to carbon assimilation. Hourly rates were converted to daily rates by assuming that average production during daylight is about $\frac{2}{3}$ the maximal rate observed around solar noon (the 4-h in situ incubations bracketed solar noon), which is an approximation to methods recommended by Vollenweider (1974a). Losses of algal carbon to grazing and algal respiration were estimated from dark-bottle rates. We multiplied oxygen consumed by a respiratory quotient of 1.0 (Strickland and Parsons 1968) to convert oxygen consumption to hourly carbon losses (assumed constant over 24 h).

Reservoir Sediment Study

To evaluate algal accumulations in the reservoir sediments, we divided the main pool of Red Rock Reservoir into four longitudinal zones (Fig. 2), and 15 sites were picked randomly from each zone. Core samples were then collected from each of these sites using a free-falling core sampler. Water depth was recorded at each site. The U.S. Army Corps of Engineers had previously measured average sediment accumulation rates on seven transects overlaying the study area (summarized by Kennedy et al. 1980), and linear interpolation between these sediment transects yielded average sediment accumulation rates at each of the points sampled here.

The top 3 cm of each core sample was analyzed for dry weight, ash-free weight, and phytopigments. The layer was well mixed, and all analyses were then performed in triplicate. Pigments were determined using a modification of Yentsch and Menzel's (1963) technique for chlorophyll analysis and using Strickland and Parsons' (1968) equations for acetone-extracted phaeophytin. Wet weight and specific weight were used to express concentrations on a sediment weight and volume basis. We computed a conservative estimate of net pigment flux (micrograms per square centimetre per year) by multiplying sediment pigment concentration (micrograms per milligram) by specific weight (milligrams per cubic centimetre) and sedimentation rate (centimetres per year). Dividing annual pigment flux for each zone by 365 d/yr and the average for integral water-column chlorophyll (milligrams per square centimetre) gave relative specific sinking rates (per day).

For diatom analysis, sediment subsamples were cleaned using a modification of Van der Werff's (1953) oxidation technique. Cleaned samples were then suspended in 30%

glycerol and the volume adjusted to obtain a diatom concentration of about 200 valves/μL. A 5.0-μL portion of this final suspension was dried on a coverslip (by gradual heating to 350°C over a 10-min period), mounted in Hyrax, and then examined under oil immersion at 1500×. Each unbroken valve within the aliquot was identified to genus when possible and assigned to one of nine size categories based on a measurement of the largest linear dimension. Approximate diatom biovolumes were computed by assuming that centric frustules have a height equal to their radius and that pennate frustule height is ¼ the greatest linear dimension. We then used original subsample weight, total volume of the glycerol suspension, and volume of the counted aliquot to convert valve counts to concentrations in the original wet sediment. We estimated diatom flux into the sediments (microlitres per square centimetre per year) by multiplying diatom biovolume in the sample (microlitres per milligram) by sediment specific weight (milligrams per cubic centimetre) and sedimentation rate (centimetres per year).

Chlorophyll Size-Fractionation and Algal Sinking Experiments

Differences in phytoplankton size distributions between upstream and downstream sections of Red Rock Reservoir were measured by size-fractionation. Reservoir water samples were size-fractionated by gravity or vacuum filtration (20 mm Hg) through a series of Nitex screens (80, 53, 25, 10 μm nominal pore size). After passage through each screen, a subsample (50–500 mL) was taken from the filtrate for chlorophyll analysis. The remainder of the filtrate was passed through the next smaller screen. Total chlorophyll was determined on an unscreened sample and the concentration in each of five size categories (>80, 80–53, 53–25, 25–10, <10 μM) was calculated by difference.

Calm-water sinking of phytoplankton assemblages from Red Rock Reservoir was measured with a settling chamber technique similar in principle to that of Eppley et al. (1967b), but using ^{14}C rather than conventional photometric or microscopic methods to follow algal movements. Use of a radiotracer gave high detection sensitivity and allowed discrimination between actively growing algae and dead material (for detailed description of apparatus see Søballe 1981).

Sinking experiments were performed in late summer 1980 (27 August, 9 September, 17 September, 1 October). Water samples (20 L) were collected from 0.5 m below the surface at the headwater and near-dam stations (I-1 and I-3, Fig. 2) and returned immediately to the laboratory (about 2-h transit time). Replicate settling chambers, filled with water sample, were maintained at ambient lake temperature for a 14- to 16-h settling period. The contents in the upper half of each chamber (350 mL) were then gently aspirated into collecting flasks. The drawn-off sample and the bottom layer were then separately shaken, and 200 mL from each of these two layers was inoculated with 1.5 MBq of $NaH^{14}CO_3$ solution (New England Nuclear). All bottles in an experiment were inoculated from one ampoule. Inoculated samples were incubated under 300 $\mu Ei \cdot m^{-2} \cdot s^{-1}$ for 6 h at the same temperature as in the settling phase. The ^{14}C-labelled samples were size-fractionated in the same fashion as in the chlorophyll analysis, with final filtration into 0.45 μm membranes. Activities on HCl-fumed filters were measured by liquid scintillation counting (Research Products International Corp. scintillation cocktail No. 3a20, Beckman model DPM-100 scintillation counter). Total uptake activity was determined on unscreened aliquots and in each of five size fractions (>80, 80–53, 53–25, 25–10, <10 μm) by difference.

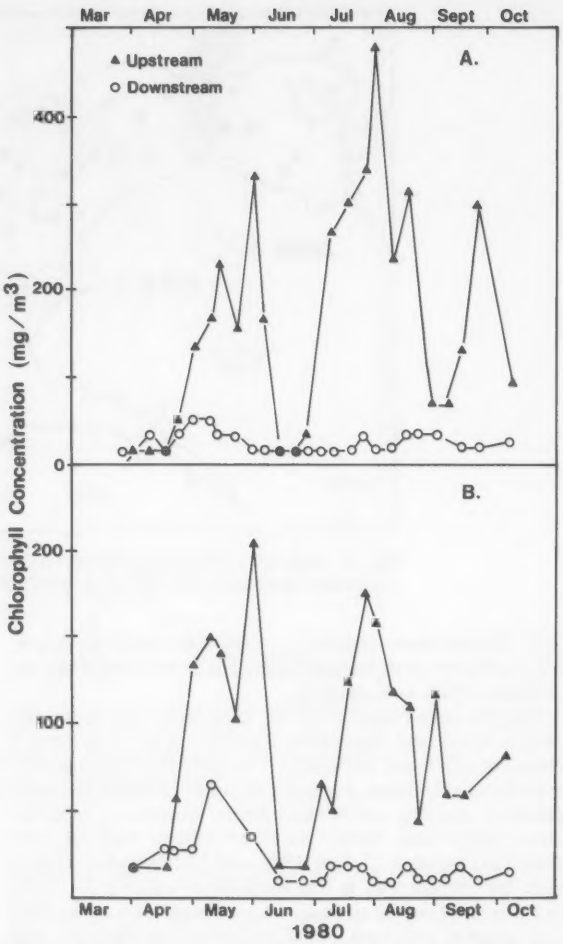

FIG. 3. Comparison of chlorophyll *a* concentrations above and below the Des Moines River impoundments. (A) Saylorville Reservoir; (B) Red Rock Reservoir.

Partitioning of ^{14}C uptake activity between the upper and lower halves of the settling chambers gave an estimate of the sinking fraction (portion of activity transferred from upper to lower chamber segment), which represents susceptibility to sedimentation rather than actual sinking rates.

Results

Reservoir Influences on Riverine Algal Biomass

On most sampling dates there was a dramatic difference in the concentrations of algal pigments in the inflows and outflows of the two reservoirs (Fig. 3). River-borne algae were removed as the water passed through the reservoir pools, and this removal altered the relationships previously reported between algal concentrations and various physical variables (i.e. chlorophyll–temperature, chlorophyll–flow, and chlorophyll–upstream streambed or watershed area).

TABLE 1. Effect of impoundments on chlorophyll (mg/m^3) vs. temperature (K) relationship at Des Moines River sites. Summary of regression analysis using the model: ln (Chl) = ln (A) + B/temperature. R_{10} (exactly analogous to Q_{10}) is the proportional change in Chl per 10 K increase.

Site	Intercept ln (A)	Slope B[a]	R_{10}	Correlation r	P
		Above impoundment			
R-10	30	−7000	2.6	−0.68	0.0001
R-1	30	−8000	2.7	−0.62	0.0001
		Below impoundment			
R-5	4	0	1.1	−0.10	0.67
R-6	16	−3600	1.6	−0.55	0.0007
R-7	20	−4500	1.8	−0.71	0.0001
I-1	20	−4000	1.7	−0.42	0.02
R-9	−8	3000	0.6	0.49	0.01

[a]Comparison of above vs. below impoundment sites; H_0: slope of the temperature response (or R_{10}) is the same above and below the impoundments. $F_{1,224} = 18.7$; $P < 0.001$; error mean square = 0.73.

TABLE 2. Effect of impoundments on chlorophyll (mg/m^3) vs. flow (m^3/s) relationship shown by regression analysis. Model: 1/Chl$_0$ = A + (B·discharge). Chl$_0$ is chlorophyll concentration divided by the harmonic mean at each site. Intercepts significantly different from zero are listed.

Site	Intercept A	Slope B[a]	Correlation r	P
		Above impoundment		
R-10	—	0.13	0.62	0.0001
R-1	—	0.07	0.74	0.0001
		Below impoundment		
R-5	1.0	0.003	0.32	0.06
R-6	—	0.006	0.59	0.0002
R-7	—	0.010	0.74	0.0001
I-1	—	0.010	0.78	0.0001
R-9	1.0	0.003	0.30	0.12

[a]Comparison of above vs. below impoundment sites; H_0: slope of flow response (B) is the same above and below the impoundments. $F_{1,220} = 69.8$; $P < 0.0001$; error mean square = 5.49.

For the upstream stations above the main-stem reservoirs, the relationship between algal concentration and temperature observed by Kilkus et al. (1975) could be described by an Arrenhius type equation:

$$(1)\quad \text{Chl} = A \exp(B/T)$$

where Chl is the measured chlorophyll concentration (milligrams per cubic metre), A and B are fitted constants, and T is the absolute temperature (kelvin). Algal growth rates have been successfully modelled this way (e.g. Goldman and Carpenter 1974), and river chlorophyll concentration should be growth related.

The fit is relatively good for the stations (R-1 and R-10) above the impoundments (Table 1), but for those stations immediately below, the temperature relationship was either not significant or negative. The latter situation resulted from more efficient removal of algal biomass during reservoir transit at higher water temperature as demonstrated for both reservoirs by regression of instantaneous net growth rate (μ) on water temperature. We calculated μ as

$$(2)\quad \mu = [\ln(\text{Chl}_d/\text{Chl}_u)]/t$$

where Chl$_d$ = chlorophyll concentration at the dam, Chl$_u$ = chlorophyll concentration directly above the reservoir, and t = theoretical hydraulic retention time (days). Regression shows a significant ($r = -0.57$; $P < 0.01$) negative effect of temperature (degrees Celsius) at both impoundments. Neither impoundment differs significantly ($P < 0.86$) from the pooled regression ($\mu = 0.045 - 0.005T$). At no river sites below Saylorville dam was the chlorophyll–temperature response as great as at the above-impoundment sites. The overall effect of the reservoirs was to weaken or uncouple the chlorophyll–temperature relationship downstream.

Reservoir removal of algal biomass also modified the downstream riverine relationship between chlorophyll concentration and flow. In reaches of the Des Moines River unaffected by impoundment and as found elsewhere (reviewed by Hynes 1970), standing crop (chlorophyll a (milligrams per cubic metre)) was inversely related to river discharge (cubic metres per second). We used a dilutional model to describe this:

$$(3)\quad \text{Chl} = (C_0 \cdot Q_0)/(Q_0 + Q_a)$$

where Chl = chlorophyll concentration at a given flow (Q), C_0 = base-flow concentration of chlorophyll (theoretical), Q_0 = base-flow discharge (theoretical), and Q_a = increase in discharge above base flow.

Because $Q_0 + Q_a = Q_t$ (the total observed discharge), substituting and rearranging yields

$$(4)\quad C_0/\text{Chl} = Q_t/Q_0.$$

C_0 and Q_0 are unknown, but for better comparison between river sites we used the harmonic mean of chlorophyll concentration at each site as a measure of C_0. Equation 4 could then be fitted by regression to the chlorophyll–flow data (Table 2).

Base flow (Q_0) increases downstream; thus, from equation 4, greater changes in flow volume should be required to produce equivalent dilutional effects at more downstream sites. The two stations (R-10 and R-1) not influenced by impoundment followed this pattern. The decrease in the regression slope ($1/Q_0$) between these two stations is roughly proportional to the increase in either watershed area (8910 vs. 14 700 km^2) or average discharge (28 vs. 70 m^3/s). Below the impoundments, however, this riverine pattern disappeared.

The chlorophyll–flow correlation was not significant at R-5 and, unlike the unimpounded reaches, the regression slope significantly increased (instead of decreased) farther downstream (Table 2). At these downstream sites the changing regression slope is clearly not reflecting increases in river volume, but may indicate recovery from reservoir influences. To test whether this recovery results from unimpounded tributaries joining the river downstream (rather than from in-river production), we used an additive model to predict chlorophyll concentration at station R-6 from the concentrations and flows at the two contributing upstream sites (R-10 and R-5):

$$(5)\quad C_6 = (C_5 \cdot Q_5 + C_{10} \cdot Q_{10})/(Q_{10} + Q_5)$$

where C_6, C_5, and C_{10} are concentrations at sites R-6, R-5, and R-10, respectively, and Q_5 and Q_{10} are river discharge measured at sites R-5 and R-10, respectively.

TABLE 3. Algal trapping characteristics of Des Moines River impoundments. Instantaneous loss rates are ln ([upstream]/[downstream]) divided by mean retention time (calculated by dividing reservoir volume by average outflow). Estimates of daily rates for Saylorville are highly approximate, since upstream site is 30 km above the reservoir at normal pool elevation.

	Saylorville Reservoir		Red Rock Reservoir	
	Mean Chl (mg/m^3)	Export (kg/d)	Mean Chl (mg/m^3)	Export (kg/d)
River station above impoundment	160	517	77	590
Midpool site	62	267	42	350
River station below impoundment	24	137	20	210
Overall trap efficiency	85%	74%	74%	65%
Average instantaneous loss rates				
Upstream to midpool (d^{-1})	0.23	0.18	0.30	0.26
Midpool to outlet (d^{-1})	0.07	0.05	0.09	0.06
Overall (d^{-1})	0.12	0.08	0.12	0.09

This model performed well (observed concentration = 0.1 + 0.88·predicted value; $r = 0.84$; $P < 0.0001$; intercept not significantly different from zero). There are no major tributaries between these sampling points; the flow at R-6 is essentially the sum of the flows at R-10 and R-5. Likewise, the chlorophyll concentration at R-6 does not differ significantly from expectation based upon the contributing flows. This indicates that either no change in chlorophyll concentration occurs between the sampling points or (the unlikely possibility) that the loss over one 20- to 30-km river reach is exactly balanced by the gain in the other.

We examined the impact of the Des Moines River impoundments on algal exports by applying Swanson and Bachmann's (1976) model for unimpounded Iowa rivers. This model predicts chlorophyll export (calculated by multiplying chlorophyll concentration by river discharge volume) from upstream streambed and drainage area. In this model, removal of algal biomass contributed from upstream is equivalent to deleting a portion of the upstream watershed. We therefore used reservoir removal efficiencies (Table 3) as a basis for subtracting 74% of the drainage area above Saylorville dam from the drainage area of downstream sites, and we likewise subtracted 65% of the Red Rock drainage area (already reduced by 75% of Saylorville's drainage) from the site below Red Rock dam. This adjustment (effectively moving the sites upstream a fixed amount) brought the chlorophyll export per unit drainage area (kilograms per day per square kilometre) for the downstream sites into good agreement with both Swanson and Bachmann's (1976) predictions and our own upstream sites (Fig. 4). In terms of this model, the Des Moines River impoundments have reset downstream sites to an upstream condition. The magnitude of this reset is a function of each reservoir's algal trapping efficiency, and the impact of each reservoir in the series is cumulative.

Algal losses increased with reservoir retention time (Fig. 5), and Saylorville reservoir with a longer average retention time trapped (on average) a greater fraction of the inflowing algal load, but instantaneous net removal rates averaged about the same at the two impoundments (Table 3; Fig. 5). When we calculated average trapping efficiencies from mean chlorophyll concentrations, we arrived at a slightly higher estimate than if we had used export values (Table 3) because mean concentration, unlike mean export, is weighted toward low flow during

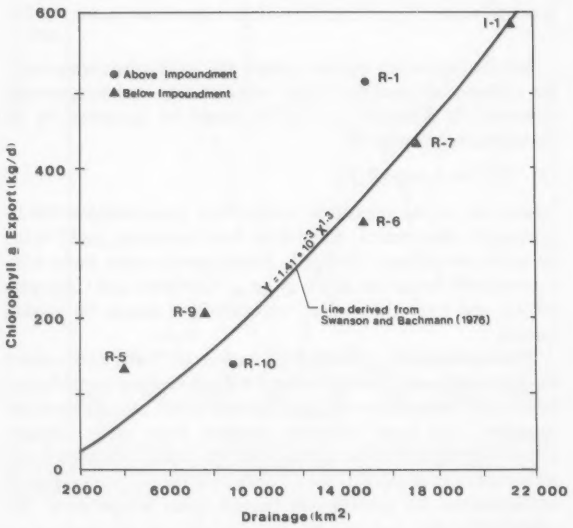

FIG. 4. Mean chlorophyll export (kg/d) vs. upstream drainage area (km^2) at river sites. Drainage areas of sites below the impoundments have been reduced to reflect the phytoplankton trap efficiency of upstream reservoir(s).

which river chlorophyll concentrations and reservoir removal efficiencies are both maximal.

Notably, the daily loss rate (slope in Fig. 5) within each impoundment is not constant ($P < 0.0002$); the loss rate decreases as retention time becomes longer (Fig. 5). No difference is demonstrated in loss rates between the two impoundments at equivalent retention times ($P < 0.75$).

Loss Processes Within the Impoundments

The dramatic loss of algal biomass across the Des Moines reservoirs is intriguing. Although nitrogen and phosphorus levels in this river–reservoir system are extremely high, chlorophyll yields are well below the predictions of regression models based on total phosphorus (e.g. Jones and Bachmann 1976) or total phosphorus and nitrogen (Smith 1982). Chlorophyll

TABLE 4. Comparison of Des Moines River chlorophyll concentrations with predictions of empirical regression models. Jones and Bachmann (1976): log (Chl) = −1.09 + 1.46 log (TP). Smith (1982): log (Chl) = −1.51 + 0.653 log (TP) + 0.548 log (TN), where TP is total phosphorus (mg/m^3) and TN is total nitrogen (mg/m^3).

	Site							
	R-10	R-1	R-3	R-5	R-6	R-7	I-1	R-9
Mean total N (mg/m^3)	9200	8520	8170	8020	8530	7990	—	7030
Mean total P (mg/m^3)	313	297	197	158	403	426	—	214
N:P ratio	29.4	28.7	41.5	50.8	21.1	18.8	—	32.9
Mean Chl (mg/m^3)	98	160	62	24	45	51	77	20
Predicted Chl (mg/m^3) (Jones and Bachmann 1976)	357	331	181	131	517	562	562[a]	204
Actual:predicted	0.27	0.48	0.34	0.18	0.09	0.09	0.14	0.10
Predicted Chl (mg/m^3) (Smith 1982)	195	182	136	117	221	218[a]	218	131
Actual:predicted	0.50	0.88	0.46	0.20	0.20	0.23	0.35	0.15

[a]Based on nitrogen and phosphorus data from upstream site R-7.

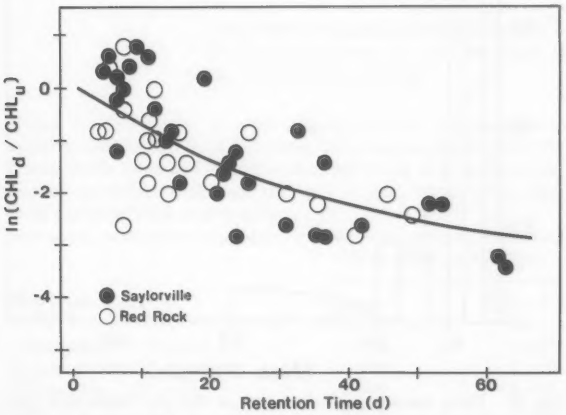

FIG. 5. Effect or retention time on phytoplankton losses in the Des Moines River impoundments. Separate regression lines for each impoundment do not differ significantly ($P < 0.75$) from the pooled regression line ($Y = -0.077X + 0.0005X^2$). Slope of this line estimates instantaneous daily growth rate.

concentrations diverged further from these predictions upstream to downstream (Table 4).

In each reservoir the percentage of phytoplankton biomass lost was nearly equal across the upstream and downstream segments (Table 3). To be consistent with longer retention times in the downstream segments (8 d vs. 2 d at Red Rock; 12 d vs. 4 d at Saylorville) loss rates there must be 3 to 4 times lower than in the upstream segments. This decrease in loss rate from upstream to downstream directly opposes the trend expected from light availability, productivity measurements, or zooplankton abundance. Water clarity increases downstream in both impoundments; however, a simultaneous increase in total depth (equal to mixed depth in these systems) results in no improvement in light availability. In fact, productivity data from Red Rock Reservoir (Table 5) demonstrated that loss rates related to respiration (light limitation) increased downstream. Zooplankton surveys at Red Rock Reservoir (Asch 1971; McGrath 1973) have shown a distinct maximum in zooplankton abundance (and hence grazing) near the dam.

Localized filter-feeding by gizzard shad (*Dorosoma cepedianum*) could contribute to increased algal losses in the upstream portion of these reservoirs, but this cause seems unlikely. The filter-feeding impact of these fish is limited to large particles (>70 μm, Drenner et al. 1982), and size-fractionation data indicate that although algae > 53 μm declined at Red Rock (Fig. 6), phytoplankton in the 25- to 53-μm size fraction sustained greater losses.

Rapid sedimentation of river-borne algae is consistent with the data. Phytoplankton sinking should be maximal where the turbulent river first enters the impoundment, and sinking losses should diminish after susceptible algae settle out. Coupling of sinking losses upstream with light limitation and grazing downstream gives the multiphase process suggested by the upstream-to-downstream reduction in algal loss rate (Table 3) and could also explain the leveling off of algal loss rate at longer retention times (Fig. 5). We attempted to evaluate this mechanism using data from Red Rock Reservoir.

TABLE 5. Algal biomass budget for two segments of Red Rock Reservoir based upon data averaged over the study period. River inlet is region between stations I-1 and I-2. Near-dam region extends from station I-2 to I-3. Sinking loss is the sum of chlorophyll loss rate (d^{-1}) and net production rate (d^{-1}). Expected C:Chl range is 25–100.

	Reservoir segment	
	River inlet	Near dam
Morphometry		
Surface area (ha)	1 050	1 130
Mean depth (m)	1.75	6.0
Chlorophyll data		
Total standing crop (kg)	1 200	1 800
Import (kg/d)	590	350
Export (kg/d)	350	210
Net loss (kg/d)	240	140
Loss rate (d^{-1})	0.20	0.08
Productivity data (carbon)		
Gross carbon (kg/d)	11 700	10 000
Dark-bottle (kg/d)	11 600	25 700
Net carbon (kg/d)	100	−15 700
Estimated specific sinking loss (d^{-1})	$0.20 + \frac{0.08}{\text{C:Chl}}$	$0.08 - \frac{8.7}{\text{C:Chl}}$

We examined first the correlation between algal loss rates and productivity. Both Red Rock and Saylorville reservoirs are highly turbid (Secchi depth usually less than 0.5 m), and light limitation is likely in the deeper portion of both reservoirs. There was no correlation ($r = -0.2$; $P < 0.37$) between chlorophyll-specific net oxygen production (grams O_2 per milligram Chl per day) and instantaneous chlorophyll-specific loss rate (per day) across the upstream half of Red Rock Reservoir, but for the downstream segment the negative correlation was significant ($r = -0.5$; $P < 0.02$). A significant negative correlation ($r = -0.5$; $P < 0.02$) between production and instantaneous loss rate was also produced when the reservoir was treated as a single unit between stations I-1 and I-3. Lag correlation may have improved this analysis, but it was not feasible with a sampling interval (weekly) approximately equal to reservoir retention time.

We used weekly productivity and physical–chemical data to calculate an average algal biomass (chlorophyll *a*) budget for Red Rock Reservoir. Conversion between oxygen production and chlorophyll units introduces large uncertainties, so results are expressed as a function of the carbon to chlorophyll ratio (Table 5).

Production and respiration in the upstream segment were nearly balanced ($P:R = 1.01$), which made the budget calculations insensitive to the carbon to chlorophyll ratio, and we estimated sinking losses of 0.2/d for this segment. A mean segment depth of 1.8 m converted this rate to a sinking velocity of 36 cm/d, which is well within the normal range (Smayda 1970). A different situation existed downstream. The budget calculations showed that with a carbon to chlorophyll ratio less than 120, respiration and grazing (without any sinking losses) accounted for the net loss of chlorophyll (0.07/d) across the downstream segment. Direct measurement of the algal carbon to chlorophyll ratio was impractical because of excessive organic debris in the river, but literature values for high-nutrient, low-light conditions are in the range 20–40 (Parsons et al. 1961; McAllister et al. 1961; Eppley et al. 1967a; Eppley 1968; Eppley et al. 1971; Perry 1976). The budget calculations suggest that algal sedimentation was a major loss upstream, while (in agreement with the correlation analyses) grazing and respiration removed additional biomass downstream. The sediment data that follow support this conclusion.

Phytopigment analysis of Red Rock Reservoir sediment cores showed algal sedimentation rates declining significantly from upstream to downstream (Table 6). These rates are 25–50% less than the biomass budget value for the upstream segment, but the rates agree with the budget calculation in showing nonsignificant sinking downstream ($t = 0.7$; $P < 0.8$). The pigment data underestimate algal sinking for two reasons. First, other chlorophyll derivatives in the sediments have lower specific absorption coefficients than the phaeophytin *a* value used in our calculations (Brown 1968), and second, chlorophyll destruction (conversion to colorless derivatives) occurs in both the sediments and the water column.

Sedimented pigments should also underestimate the difference in algal sinking between upstream and downstream due to resuspension and transport from upstream sediments and enhanced fecal deposition of pigments downstream where zooplankton abundance is greatest (Asch 1971; McGrath 1973). One process counters this trend. Total sediment accumulation in Red Rock Reservoir is more rapid upstream than down (Table 6), so the top 3 cm of sediment core (the portion analyzed for pigments) from the upstream sites is more recent (estimated

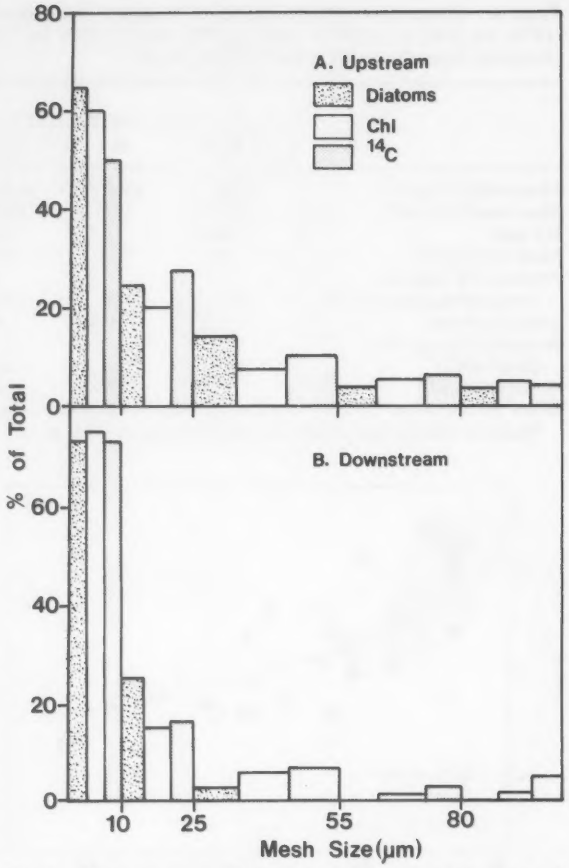

FIG. 6. Three measures of algal size in the (A) headwaters and (B) near-dam sections of Red Rock Reservoir. Chlorophyll and ^{14}C uptake are based upon water column sampling. Diatom size distribution is from sediment core analysis.

average ages are 50, 120, 150, and 220 d for zones 1 to 4, respectively). Therefore, a pigment destruction rate of 0.02/d could produce the observed longitudinal trend without differential algal sinking between zones. However, chlorophyll degradation products are stable and remain detectable after thousands of years in aphotic and anaerobic sediments (Vallentyne 1955); thus, rates on the order of 2%/d are extremely unlikely.

Analysis of sedimented diatoms also indicated enhanced algal sinking in the upstream half of Red Rock Reservoir (Table 6). These data gave an approximate check on the algal sedimentation rates derived from both the biomass budget and sedimented pigments. Assuming that algal carbon is 10% of algal wet weight (Vollenweider 1974b), a specific weight of 1.0 for algal cells, and a carbon to chlorophyll ratio of 40 (discussed previously), we used sediment diatom biovolumes to approximate the rates of diatom-associated chlorophyll sinking (Table 6). As with pigments, fecal deposition and resuspension/transport could reduce upstream–downstream differences. We counted only unbroken diatom valves and this should have somewhat excluded fecal diatom contributions from this analysis, but the magnitude of resuspension, transport, and settling of dead but intact organisms is unknown. We assumed that diatom growth in these aphotic sediments was negligible.

TABLE 6. Longitudinal changes in phytopigment and diatom sedimentation at Red Rock Reservoir. Average loss rates based upon fraction of mean integral chlorophyll (mg/m^2) deposited daily from the water column in each zone.

Zone	Mean depth (m)	Sedimentation rate (cm/yr)	Pigments		Diatom valves[a]	
			Flux ($\mu g \cdot cm^{-2} \cdot yr^{-1}$)	Loss rate (d^{-1})	Biovolume flux ($\mu L \cdot cm^{-2} \cdot yr^{-1}$)	Loss rate (d^{-1})
1	1.1	20.8	416	0.15	221	0.21
2	2.3	9.1	290	0.06	302	0.19
3	4.3	7.1	185	0.03	145	0.06
4	5.5	5.0	125	0.02	83	0.04
Analysis of variance[b]						
F			6.67	13.97	7.17	—
P			0.001	0.0001	0.01	—
Error mean square			27 843	0.004	370	—
Degrees of freedom			3,38	3,38	1,20	—

[a]Loss rate is estimated chlorophyll loss due to diatom sedimentation.
[b]H_0 for pigment data: all zones are equal; H_0 for diatom biovolumes: zones 1 and 2 pooled are equal to zones 3 and 4 pooled.

TABLE 7. Differences in algal sinking between size-fractions at opposite ends of Red Rock Reservoir. Data are proportion (p) of ^{14}C transferred to lower half of settling chamber during 15 h. Analysis performed on arcsin transformed (arcsin $\sqrt{p}$) data. Means below have been converted back to proportions.

Size class	Mean amount settled (p)	
	Station I-1	Station I-3
Ultraplankton (<10 μm)	0.196	0.223
Nanoplankton (10–53 μm)	0.490	0.519
Netplankton (>53 μm)	0.644	−0.014
Total[a]	0.550	0.330
Analysis of variance[b]		
F	7.65	3.65
P	0.01	0.07
Error mean square	750	539
Degrees of freedom	1,48	1,31

[a]Total activity settled at station I-1 is significantly different from station I-3; $F_{1,31} = 23.13$; $P < 0.0001$; error mean square = 56.6.
[b]H_0: ultraplankton settling is not different from larger size classes.

TABLE 8. Comparison between mean sizes (greatest linear dimension) of diatoms in four sediment zones at Red Rock Reservoir.

Analysis of variance					
Source	df	*F*	*P*	Zone	Mean size (μm)
Zones	3	12.65	0.0001	1	16.6
Contrasts				2	12.8
1 and 2 vs. 3 and 4	1	24.04	0.0001	3	10.6
1 vs. 2	1	13.50	0.002	4	11.4
3 vs. 4	1	0.39	0.54		
Error	20	Mean square 3.2			

To further substantiate the algal sedimentation patterns at Red Rock Reservoir, we conducted three settling experiments during August and September 1981 when a marked uplake–downlake chlorophyll gradient persisted at this impoundment (Fig. 3). Analysis of the pooled results showed significantly greater portions of the total ^{14}C uptake activity settling from the river-inlet samples than from near-dam samples over 15 h (Table 7). Size-fractionation in these experiments indicated an uncoupling of sinking rate from algal size during reservoir transit. In river-inlet samples, the >10-μm size classes settled significantly more than did the <10-μm size class (Table 7), but in the reduced phytoplankton assemblage reaching the dam, the few phytoplankton >53 μm showed slight positive bouyancy and the difference between nanoplankton (10–53 μm) and ultraplankton (<10 μm) was only marginally significant (Table 7). This suggests that rapidly sinking forms are selectively removed from all size classes as the population transits the reservoir.

In addition to these experiments, chlorophyll size-fractionation showed a 20–30% downstream reduction in mean and median size (means: 21 μm upstream vs. 14.6 μm downstream ($t = 3.3$; $P < 0.01$); medians: 13.5 μm upstream vs. 8.0 μm downstream ($t = 2.5$; $P < 0.02$)). Sedimented diatoms (Table 8) showed a similar pattern. Algal sinking speed generally increases with size (Smayda 1970), and sinking losses should produce a longitudinal size reduction in the diatom-dominated assemblage entering Red Rock Reservoir. Processes other than size-selective sinking, however, could have contributed to this pattern.

Discussion

Contrary to common descriptions of algal abundance in river–reservoir systems (e.g. Cushing 1964; Hynes 1970; Wetzel 1975; Baxter 1977; Ward and Stanford 1983), the reservoirs of the Des Moines River function as in-river processors that reduce rather than augment the river-borne algal load. Longitudinal decreases in algal abundance have been observed in other riverine impoundments (Round 1981; Jones

and Novak 1980; Vandenberg 1978; Marzolf and Osborne 1972) and are not unique to these Iowa reservoirs. At Red Rock Reservoir, loss of algal biomass parallels a longitudinal shift in trophic state. This reservoir is weakly autotrophic uplake but strongly heterotrophic downlake. Saylorville Reservoir should be similar but no productivity data are available to test this.

Algal sedimentation in Red Rock Reservoir is not simply a loss of benthic algae scoured from the upstream river bed. Although headwater benthos are undoubtedly among the several sources for riverine inocula, observed densities (chlorophyll *a* > 400 mg/m^3) in the river testify to extremely successful algal growth in suspension. Euplanktonic forms are prevalent (Drum 1981) and the term potamoplankton seems appropriate to this river-borne assemblage. Although these algae are extremely successful in the river, transition to lentic conditions is catastrophic. Light limitation accounts for part of the in-reservoir loss of algal biomass, but reduction in turbulence (and subsequent algal sedimentation) is equally significant. Algal sedimentation in Red Rock Reservoir is rapid: virtually all susceptible algae are removed in less than a week, and a majority may settle within hours after entering the impoundment. Domination of the Des Moines River by diatoms (Starrett and Patrick 1952; Drum 1981; also reviewed by Swanson and Bachmann 1976) makes this assemblage particularly susceptible to sinking. Flocculation of river algae with suspended clay particles may further contribute to sedimentation losses (cf. Avnimelech et al. 1982).

Rzóska et al. (1955) found that the few "adventitious" benthic algae carried by the Nile settled out upon entry into an impoundment. This settling out was followed by longitudinal development of a dense lentic phytoplankton. By comparison, the Des Moines River carries a dense potamoplankton that likewise settles out during transition to lentic conditions, but lentic populations do not develop subsequently because the lentic situation is unsuitable (light limited) and too brief (because of rapid advection).

Reservoirs often exhibit longitudinal gradients in the biological and physical factors (e.g. turbulence, light, temperature, nutrients, predation) that regulate both phytoplankton production and species succession, and the longitudinal phytoplankton shifts associated with these gradients may mimic temporal succession. For example, the longitudinal sedimentation of algae in Red Rock Reservoir is analogous to seasonal sinking losses observed by Lund (1954), Jassby and Goldman (1974), Knoechel and Kalff (1975), and Crumpton and Wetzel (1982).

As expected from the relationship between size and sinking speed (Smayda 1970; Walsby and Reynolds 1980), transit of Red Rock Reservoir alters the size structure of the phytoplankton assemblage. This algal size gradient suggests that Red Rock Reservoir, and other similar impoundments, may be good sites for examining both size-selective processes and the role of phytoplankton size in energy transfer to higher trophic levels.

Algal biomass in the Des Moines River impoundments is uncoupled from the chlorophyll–phosphorus/nitrogen relationships seen in most natural lakes. Empirical chlorophyll–nutrient models assume conditions that allow algal biomass to approach phosphorus or nitrogen limitation, but here, nonnutrient factors are major determinants of phytoplankton abundance. Similar conditions elsewhere may help explain Canfield and Bachmann's (1981) finding that chlorophyll yields (per unit phosphorus) are significantly lower and less predictable in reservoirs than in natural lakes.

Because phytoplankton crop is more closely tied to advective inputs and subsequent losses than to nutrient limitations, the Des Moines River reservoirs, and perhaps other riverine impoundments, are better viewed as in-river processors that modify the riverine algal load rather than as lakes with a large riverine tributary. Short retention time in these impoundments does not imply dilution of nutrients or washout of phytoplankton standing crop (cf. Dickman 1969), but rather a time limit for biological responses to the changing conditions encountered during transit. Models that predict lake trophic status on the basis of nutrient limitations without regard to biological response time (e.g. Dillon 1975; Jones and Bachmann 1976; Smith 1982) are inappropriate to this situation.

In the Des Moines River above the main-stem impoundments, the algal concentration (chlorophyll *a*) is dependent upon water temperature and flow. In-reservoir removal processes that depend upon temperature and retention time tend to weaken or even reverse these patterns in the river below the dams. Vannote et al. (1980) and Ward and Stanford (1983) suggested that impoundments act as "reset" mechanisms that cause river transport patterns to be shifted toward the headwaters or seaward depending upon the reservoir type and location. Our study provides evidence from an unforested agricultural watershed to support that view. Average algal export below the Des Moines River dams is reset to resemble upstream reaches. Saylorville Reservoir's reset of algal export extends more than 65 km downstream and reaches past Red Rock Reservoir. The cumulative effect on algal transport of these two reservoirs indicates that these are not localized perturbations. Stream order does not change appreciably between these two reservoirs, so we could not test for effects related to reservoir location, but removal of phytoplankton in this system is clearly tied to the nature of the upstream watershed, which exports both inorganic suspended particles and dense diatom populations. It remains to be demonstrated whether the algal size reduction associated with reservoir transit comprises a reset to upstream or downstream conditions.

Acknowledgments

This work was partially supported by funding from the U.S. Army Corps of Engineers, Waterways Experiment Station, Vicksburg, MS, and Rock Island District, Rock Island, IL, via contracts DACW 25-78-C-0077, DACW 25-80-C-0002, DACW 25-80-C-0008, and DACW 25-80-0009 to Prof. E. R. Baumann, Department of Civil Engineering and Engineering Research Institute, Iowa State University, Ames, IA 50010. Comments and discussion from B. L. Kimmel were extremely helpful, and we thank S. M. Adams for his review. Oak Ridge National Laboratory (ORNL) is operated by the Martin Marietta Energy Systems, Inc. under contract DE-AC05-840R21400 with the U.S. Department of Energy.

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Cross Correlations Between Reconstructed Ocean Abundances of Bristol Bay and British Columbia Sockeye Salmon (*Oncorhynchus nerka*)

Randall M. Peterman

Natural Resource Management Program, Simon Fraser University, Burnaby, B.C. V5A 1S6

and Fred Y. C. Wong

Pacific Biological Station, Nanaimo, B.C. V9R 5K6

Peterman, R. M., and F. Y. C. Wong. 1984. Cross correlations between reconstructed ocean abundances of Bristol Bay and British Columbia sockeye salmon (*Oncorhynchus nerka*). Can. J. Fish. Aquat. Sci. 41: 1814–1824.

Anecdotal reports of a tendency for British Columbia sockeye salmon (*Oncorhynchus nerka*) to be low when Bristol Bay, Alaska, returns are high prompted a reconstruction of minimum abundances of sockeye resident in the Gulf of Alaska each year from the early 1950s to mid-1970s. This backwards reconstruction using Fry's virtual population analysis was done by using catch, escapement, and age structure data for each area in British Columbia and Bristol Bay. Use of more sophisticated backwards reconstruction methods was precluded by lack of age-specific annual survival rates by stock. Ocean abundances of British Columbia and Bristol Bay sockeye show significant autocorrelations at periods consistent with the cyclic dominant patterns of their largest stocks. Cross correlations at lag 0 between ocean abundances of various ages of fish from these two regions show one case of a significant inverse relation in abundances. In addition, there are significant cross correlations between British Columbia and Bristol Bay ocean abundances at various time lags, showing that cycles in their abundances are out of synchrony. This lack of synchrony persisted longer than would be expected from cyclic dominance patterns and age at maturity of British Columbia and Bristol Bay sockeye, and several alternative explanations of this asynchrony are discussed.

En raison de témoignages selon lesquels le nombre de saumons nerka (*Oncorhynchus nerka*) retournant en Colombie-Britannique aurait tendance à être faible lorsqu'il est élevé dans la baie Bristol (Alaska), nous avons entrepris de déterminer le nombre minimum de saumons qui sont restés chaque année dans le golfe de l'Alaska depuis le début des années cinquante jusqu'au milieu des années soixante-dix. Nous avons réalisé cette reconstitution par l'analyse des populations virtuelles selon la méthode de Fry en utilisant les données que nous possédions sur les prises, le nombre de poissons non capturés et la pyramide des âges dans chaque région de la Colombie-Britannique et de la baie Bristol. Il nous a été impossible de recourir à des méthodes plus perfectionnées, car nous n'avions aucune donnée sur le taux de survie annuelle dans chaque catégorie d'âge pour chacun des stocks. D'après nos données sur l'abondance en mer du saumon nerka de la Colombie-Britannique et de la baie Bristol il y a des autocorrélations significatives à des époques qui correspondent aux cycles de dominance des plus grands stocks. En étudiant les corrélations entre l'abondance en mer des poissons de diverses catégories d'âges des deux régions à la période de baisse 0, nous avons trouvé un cas de relation inverse significative. Nous avons également trouvé des corrélations significatives entre l'abondance en mer des poissons de la Colombie-Britannique et de la baie Bristol à diverses autres périodes de baisse, ce qui indique que leurs cycles ne sont pas synchrones. Cette asynchronie a persisté plus longtemps que ne le laisseraient supposer l'âge des saumons à maturité et les cycles de dominance ; plusieurs hypothèses sont avancées pour expliquer ce phénomène.

Received October 4, 1983
Accepted August 17, 1984
(J7558)

Reçu le 4 octobre 1983
Accepté le 17 août 1984

Since 1975 we have repeatedly heard speculation from salmon fisheries managers that total returns (catch plus escapement) of Bristol Bay Alaska sockeye salmon (*Oncorhynchus nerka*) are inversely related to total returns of sockeye in British Columbia in any given year. Extensive high seas tagging studies (French et al. 1976; Hartt 1980) indicate considerable overlap in space and time of British Columbia and Bristol Bay sockeye stocks (Fig. 1). The inference is frequently then drawn that some interaction among British Columbia and Bristol Bay sockeye might plausibly occur on the high seas. Such an interaction would have important implications for future salmonid enhancement plans and for any contemplated management schemes intended to fill in off-cycle years in populations that exhibit cyclic dominance.

We examine the speculations concerning potential interactions among Bristol Bay and British Columbia sockeye in two ways, first by using the catch and escapement data, and second by estimating the abundances of sockeye actually resident in the

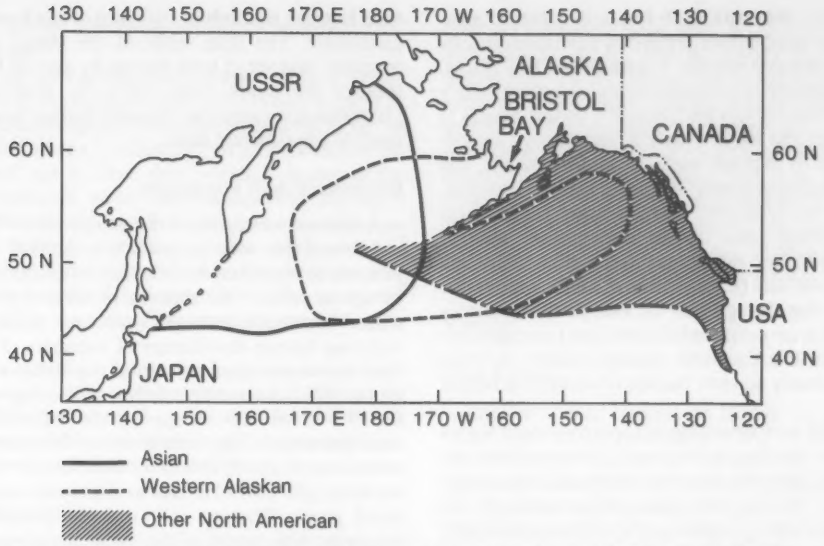

FIG. 1. General oceanic distribution of sockeye salmon from Asia, western Alaska, and other North American areas, including British Columbia (after French et al. 1976).

Gulf of Alaska in any given year (hereafter called ocean sockeye abundances). The latter approach is likely to be a better basis for analysis of potential interactions than either catch or total returns to harvest areas each year because (1) enumerations of catch and escapement occur in areas separated by several thousand kilometers and hence only indirectly represent high seas abundances, and (2) catches and escapements are affected by annual variation in age at maturity and hence may not adequately reflect changes in ocean abundances. Reconstructed populations resident in the ocean are much more appropriate for our purpose. We also document unusual patterns in Gulf of Alaska sockeye abundances and review several alternative explanations of those patterns.

Methods

In the Gilbert–Rich age notation, age 4_2 indicates the fish is in its 4th yr of life, and it entered the ocean during its 2nd yr, after rearing one winter as a fry in freshwater. Most British Columbia sockeye are sub-2 fish, but the Bristol Bay stocks have large numbers of both sub-2 and sub-3 fish.

Data Sources

To obtain ocean abundances of sockeye we use data for total returns (catch plus escapement), by age, for each statistical area in British Columbia and for each stock or district in Bristol Bay. We do not include other North American sockeye that also mature in the Gulf of Alaska because few long-term records exist for them that include age structure data. However, the omitted stocks generally are insignificant in comparison with abundances of Bristol Bay and British Columbia stocks. Based on average catch figures for 1952–75, the stocks included in our analysis comprise 80% of the total catch from North American sockeye stocks (Fredin et al. 1977). Asian sockeye stocks are also relevant because their distribution significantly overlaps that of Bristol Bay sockeye but not British Columbia fish (Fig. 1). But again, no long-term age-structured abundance data are available for total Asian sockeye returns. Catches of Asian sockeye average about 28% of total North Pacific sockeye catches (Fredin et al. 1977).

The Bristol Bay sockeye salmon catch and escapement data are available by stock or fishing district and by age. Stocks included are those of the Ugashik, Egegik, Naknek, Kvichak, Branch, Wood, Igushik, Nuyakuk, Snake, Nushagak-Mulchatna, and Togiak rivers. Catch and escapement data by age for return years 1956–80 were keypunched from summary data sheets of the unpublished sockeye salmon data book used by fisheries managers in that region (K. Parker and C. P. Meacham, Alaska Department of Fish and Game, Anchorage, AK, pers. comm.). These data are identical to those in Yuen et al. (1981) except that in addition, we include estimated Japanese high seas catches (provided by C. P. Meacham, pers. comm.), as allocated to each stock and age in proportion to the relative total returns to each river system by age. The data used here for Bristol Bay sockeye stocks include the following 15 age classes: 3_1–3_2, 4_1–4_3, 5_1–5_4, 6_2–6_4, 7_3–7_4, and 8_4. The major age groups 4_2, 5_2, 5_3, and 6_3 comprise an average of 97.8% of Bristol Bay sockeye returns. Catches (in numbers of fish) are based on commercial catch sales slips, and escapements are based on visual counts from towers, a technique that yields relatively accurate estimates of spawners (see Cousens et al. 1982). No native or sport catches are included but these are relatively minor components. Age structure is estimated from fish scales sampled from catches and escapements.

British Columbia sockeye data require several more steps to create a record of catches and escapements by age. British Columbia is divided into 30 statistical areas. Commercial catch data, by statistical area, are from the *British Columbia Catch Statistics* volumes published annually by the Department of Fisheries and Oceans (DFO), Vancouver, B.C. These catches, in numbers of fish, are estimated from fish sales slip information. Escapements are based on a series of DFO Data Reports (Fish. Mar. Serv. Data Rep. Nos. 52, 72, 79, 80, 115, 132, 140, 143, 151, 159; Can. Data Rep. Fish. Aquat. Sci. 161, 167, 183,

203, 311, 219, 222, 299, 300, 320) for each statistical area. Escapement data for areas not yet covered by published catalogs are from Fisheries Officer's records. Unlike Bristol Bay stocks, many British Columbia sockeye escapements are less accurately estimated because foot surveys are frequently used (Cousens et al. 1982). However, the major Fraser River sockeye escapements are estimated by detailed mark–recapture methods, and the second largest sockeye-producing river in British Columbia, the Skeena, also has relatively well-estimated escapements obtained at a counting fence on the Babine Lake system. Records of native Indian subsistence catch of sockeye are incomplete, but recent data (F. E. A. Wood, DFO, Vancouver, pers. comm.) show that during 1965–74, total British Columbia Indian catches (which are not included in our data) averaged less than 3% of total British Columbia sockeye returns in those years. There are virtually no sport catches of sockeye in British Columbia.

The total catch and escapement abundances by statistical area in British Columbia are then apportioned into abundances by age using published age structure data estimated from scales sampled in catches (and in some cases escapements) for the appropriate statistical areas (Anderson 1976; Bilton et al. 1965, 1966, 1967a, 1967b, 1968; Foskett 1952–57; Jenkinson et al. 1969; Jenkinson and Bilton 1970, 1971, 1972, 1973; Killick and Clemens 1963; Manzer 1976). Only the most significant age groups of British Columbia sockeye are used: 3_2, 4_1–4_3, 5_2, 5_3, and 6_3. These age groups comprise over 98% of British Columbia sockeye. The age structures given in the references above cover 1951–72 for most sampled areas and were estimated from commercial catches, with the exception of the Skeena River, which utilized test fishery data to derive a combined age structure for catch plus escapement. These data were supplemented in some years by age structure data from other test fisheries where available (areas 3 and 9) (A. D. Anderson, E. Zyblut, and M. Farwell, DFO, Vancouver). Fraser River sockeye ages are from purse-seine samples. The abundance of jacks (age 3_2 and 4_3 males) is probably underestimated in those cases where age structure is derived only from commercial gillnet samples because of gear selection for larger fish. However, jacks average less than approximately 4% of each brood year's returns, so the bias is small.

Age structures in years for which no age data exist were derived by one of the two methods: (1) age data from other areas were used, with the appropriate areas being determined by discussions with DFO area managers and by the stock interception tables regularly used as part of the Pacific Region U.S. – Canada Negotiating System (C. C. Graham, DFO, Vancouver, pers. comm.), or (2) historical average of the area's age structure, by cycle year. Abundances filled in by the latter method account for less than 1.4% of the total British Columbia returns for 1951–75. The interception table data are based on tagging studies and occasional samples taken by DFO personnel which show, for example, that catches in areas 14–20 are at least 99% Fraser River fish. Therefore, in this example, the Fraser River age structures for the appropriate years were used to fill in the missing age data for those areas. This interception table method for filling in missing ages applies to 17.9% of the total British Columbia returns over the 25-yr period covered here, but because migration routes are relatively well known from annual sampling programs, these filled in data are unlikely to cause significant bias. Indeed, Wong (1982) used two methods similar to this interception table for allocating catch interceptions to appropriate stocks, and he found little difference between methods in estimates of stock–recruitment curve parameters. The final result of the above calculations is a complete data set of total returns *by age* for British Columbia sockeye for return years 1951–75. Note that the British Columbia data cannot be extended further because of a lack of detailed age structure data.

Reconstruction of Populations

A minimum estimate of the population of British Columbia and Bristol Bay sockeye resident in the Gulf of Alaska in any year can be reconstructed from annual catches and escapements by age in each of the sections of those regions. One simply works backwards through time and through age classes, summing known abundances of members of the same brood class in a manner similar to virtual population or cohort analyses (Pope 1972). An example follows for ocean abundance, from fall 1973 to fall 1974, of age 4_2 sockeye from British Columbia statistical area 4. This abundance will be referred to here as the abundance of age 4_2 fish in ocean residence year 1974. Ocean residence year (ORY) is used to distinguish cases from return or brood years. Working only with the returns to area 4 and beginning with returns of the oldest age group, R_L, one works backwards adding the known age 6_2 returns in 1976 ($R_{6,1976}$) to the age 5_2 returns in 1975 and those to the age 4_2 returns in 1974. More generally, the minimum ocean abundance $N_{i,t}$ of a given age i in a given ocean residence year t is

$$(1)\quad N_{i,t} = R_{i,t} + R_{i+1,t+1} + \ldots + R_{L,t+L-i}.$$

This procedure is most similar to Fry's (1949) original virtual population method in that it only deals with known abundances from each cohort. Ideally, one would like to inflate the known recruits by the marine survival rate for that stock, age stanza, and year, since an abundance X is

$$X_{t+1} = x_t S \qquad \text{or}$$

$$(2)\quad X_t = X_{t+1}/S$$

where S is the survival rate for that particular age stanza and stock in that particular year. However, in this analysis, abundances are *not* divided by estimated survival rates between ages to inflate numbers back to the abundance at the previous year and age because survival rates between ocean ages are unknown for most salmon stocks. Application of the few known survival rates to the remaining stocks and ages might seriously confound interpretation of the results. This estimation procedure therefore produces a *minimum* estimate of the number of sockeye of a given age present in the Gulf of Alaska in a given year, contributed by stocks in a given statistical area. Next, the minimum abundances of the given age and year from all areas in British Columbia are summed to give a total British Columbia contribution to Gulf of Alaska sockeye. A similar procedure is followed for Bristol Bay stocks. By annually summing the minimum ocean abundances of British Columbia and Bristol Bay stocks, a minimum abundance of sockeye in the Gulf of Alaska is obtained by age, and for all ages combined.

The reconstructed ocean abundances of salmon are calculated here by age and are also summed into possible important age categories such as ages 2 + 3, 4 + 5, >2, and all ages. Because it is not clear a priori at what ages sockeye stocks might be most affected by physical or biological processes, these age groupings are used to reflect several possible types of processes by combining ages that are most similar in size and that presumably have similar effects on food supply or predators, and by

summing across several age groups to indirectly reflect total numbers of large fish.

Categories of fish with different subscripts (e.g. 5_2 or 5_3) are handled separately in the stock reconstruction to take account of the effect of the different ages at which fish entered the ocean. In other words, a group of age 5_3 fish is not carried backward in the reconstruction past age 3, since they were not present in the ocean at age 2. In addition, when total abundances of, say, age 5 fish are calculated, all fish of age 5 that are present in the ocean at that time are summed regardless of their freshwater life history. This combining procedure is justified by the findings of Ricker (1982) that "length of freshwater life (or the associated genetic effects) have a small effect on final size" of adult sockeye salmon.

In all methods described below the longest possible time series of data is used within each reconstructed abundance by age category. Different age categories thus have different sample sizes because of the incomplete brood returns at the time the last abundance by age data were available.

Descriptions of Time Series

Both British Columbia and Bristol Bay sockeye abundances exhibit wide fluctuations, so autocorrelation functions are calculated using standard methods (Box and Jenkins 1976) to determine whether there are significant cycles. Significant deviation from zero for an autocorrelation at any given lag is determined by a two-tailed t-test in which the standard error of the autocorrelation (SE_r) under the null hypothesis of no autocorrelations is the square root of $1/(N - |k|)$ (Box and Jenkins 1976, p. 34), where N is the original number of data points and k is the lag. Linear time trends in abundances are also calculated.

Comparison of Abundances

Cross correlation coefficients are first calculated between total Bristol Bay and British Columbia sockeye returns (catch plus escapement) in the same year. Then, cross correlations are calculated between reconstructed ocean sockeye abundances by ocean residence year of those two groups of stocks, by age category. As will be seen in the Results section, both Bristol Bay and British Columbia ocean sockeye abundances exhibit a periodic fluctuation, partly due to the cyclic dominance of some of their most abundant stocks (such as Fraser River stocks in British Columbia and Kvichak River sockeye in Bristol Bay). This cyclic pattern creates an autocorrelation in each time series of data so that abundances in successive years and residuals from time trends are not completely independent. Thus, in these cases the standard errors normally calculated for the cross correlations give probabilities that are too small. To allow for this time series effect on the hypothesis test for significant cross correlations, we use Bartlett's formula (given in Box and Jenkins 1976, p. 377) to calculate a corrected estimate of the standard error of the cross correlation coefficient (SE_{cr}):

$$(3)\quad SE_{cr}(k) = \mathrm{SQRT}\left[(N - |k|)^{-1} \sum_{v=-(N-2)}^{+(N-2)} r_{xx}(v) r_{yy}(v)\right]$$

where N is the total number of paired observations in the original time series, k is the lag, $r_{xx}(v)$ is the autocorrelation of time series X at lag v, and similarly for $r_{yy}(v)$. A two-tailed t-test is then used to test the null hypothesis (H_0) that the cross correlation is zero. Bartlett's formulas for standard errors of auto- and cross correlations are most applicable when sample sizes are extremely large; thus, the results of hypothesis tests here, where $n < 25$, may be slightly biased (n is $N - |k|$). Apparently, no statistician has worked out the case for the relatively small sample sizes we normally face in fish population analyses. For comparison, we report results here both from the standard hypothesis test for $r = 0$, derived without applying any correction for autocorrelation, and from the hypothesis test which uses the corrected SE_{cr} from Bartlett's formula. To test for significant lags between the Bristol Bay and British Columbia abundances, cross correlations are calculated at several lags, by age category, along with Bartlett's standard error estimate.

Results

Total Returns

Total returns of sockeye to British Columbia waters have varied between approximately 4 and 17 million and between about 3 and 60 million for Bristol Bay. Using the standard hypothesis testing method, there is a significant inverse correlation between total sockeye returns of all ages to British Columbia and Bristol Bay (Fig. 2, $r = -0.42$, $P = 0.044$). However, when equation (3) is used to account for the effect on the standard error of autocorrelations in each of the total returns time series, the correlation of -0.42 is no longer significant ($P > 0.1$). So while there is a tendency for an inverse relation between Bristol Bay and British Columbia sockeye returns, it is not significant.

Reconstructed Ocean Abundances

Features of the time series: autocorrelations

No age category of ocean abundances of Bristol Bay, British Columbia, or total Gulf of Alaska sockeye shows a significant linear time trend (all $n \geq 17$, all $P \geq 0.1$). However, several age groups show significant periodicities, as indicated by autocorrelations at various lags. All combinations of age category and lag were tested for autocorrelation, and only the significant cases

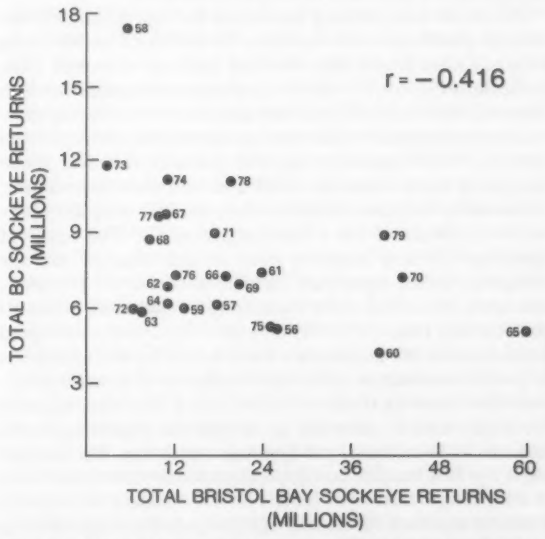

FIG. 2. Relation between total returns (catch plus escapement) of British Columbia and Bristol Bay, Alaska, sockeye salmon by return year.

are listed in Table 1. For British Columbia sockeye, significant autocorrelations occur at a lag of 2 yr (negative autocorrelations) and 4 yr (positive autocorrelation) (Table 1). The 2-yr lag results for age groups 2 + 3 and >2 are consistent with the well-documented phenomenon of cyclic dominance in Fraser River sockeye (mostly attributable to one of the stocks, Adams River), in which there typically is one very abundant or dominant year, followed by a low to moderate abundance year, and then 2 yr of extremely low abundance (Ricker 1950; Ward and Larkin 1964). Over 90% of Fraser River sockeye mature at age 4, so this gives rise to a large abundance every 4 yr. For the return years examined here, Fraser River stocks comprise 48.6% of total British Columbia sockeye returns (catch plus escapement), so it is not surprising that abundances summed across all British Columbia statistical areas also exhibit similar regular patterns (Fig. 3). The other significant British Columbia result, for abundance of age 6 British Columbia fish, largely reflects the northern British Columbia stocks (areas 1–9) which contribute most of the age 6 fish from British Columbia.

Bristol Bay sockeye also show significant autocorrelations in several age categories, positive ones at lag 5 and negative at lag 2 (Table 1). The large positive autocorrelations at lag 5 are explained by the existence of cyclic dominance in the Kvichak River stock, which normally has a dominant run every 5 yr (Rogers 1976; Mathisen and Poe 1981; Poe et al. 1977). This stock is extremely abundant, accounting for an average of 50.3% of total Bristol Bay sockeye. Other age categories have large autocorrelations but those cases are not significant.

Gulf of Alaska ocean sockeye abundances (in this paper meaning the sum of British Columbia and Bristol Bay numbers) largely reflect patterns of oscillation similar to those of Bristol Bay because these Alaskan stocks are much more abundant than British Columbia stocks (note different y-axis scales on bottom frames of Fig. 3a–3i). Only a lag of 2 yr in the age 4 + 5 category shows significant autocorrelation, and the probability is marginal ($P = 0.0496$) (Table 1).

Comparison of abundances: cross correlations

One of the most striking features of the time series of ocean sockeye abundances is the tendency for British Columbia stocks to be low when Bristol Bay stocks are high and vice versa. Note particularly Fig. 3b, 3c, and 3f–3i. Simple correlations between British Columbia and Bristol Bay abundances with no lag show that most correlation coefficients are significantly different from zero at $\alpha = 0.05$ and all are negative (Table 2). However, if one recognizes that abundances within a series are not independent, as shown by the autocorrelation analyses, then standard errors must be calculated for r from equation (3). The result of applying this new standard error is that none of the age categories shows significant correlation (Table 2). However, this result arises from use of equation (3), which sums across all possible lags from $-(N-2)$ to $+(N-2)$. Using an accepted procedure, we can also perform these tests of the null hypothesis of no cross correlation under the assumption of no autocorrelations after some lag (Fuller 1976, p. 268). In this case, equation (3) is only used by summing up through the longest lag that is assumed to be relevant, and ignoring longer lags. This longest lag is 5 yr here because no significant autocorrelation was found at a lag longer than 5 yr (Table 1). New standard errors result from this approach but the only age category that is significant is age >2 ($P = 0.036$). Thus, under the null hypothesis that there is no process that causes autocorrelations in either British Columbia or Bristol Bay abundances at lags ≥6 yr, there exists a significant inverse relation between the abundance of ages >2 from those regions, with $r = -0.77$ (Fig. 4).

TABLE 1. Significant autocorrelations for time series of reconstructed minimum ocean abundances of British Columbia, Bristol Bay, and Gulf of Alaska (British Columbia plus Bristol Bay) sockeye salmon. "Years" column shows length of original time series. Sample size at the stated lag is given by n.

Age category	Years	Lag (yr)	n	Auto-correlation	SE	P
British Columbia						
6	1951–75	4	21	0.467	0.218	0.047
2 + 3	1951–72	2	20	−0.558	0.224	0.024
>2	1951–72	2	20	−0.511	0.224	0.038
Bristol Bay						
2 + 3	1956–76	5	16	0.565	0.250	0.043
4 + 5	1956–76	2	19	−0.582	0.229	0.022
All ages	1956–76	5	16	0.583	0.250	0.038
Gulf						
4 + 5	1956–73	2	16	−0.538	0.250	0.050

In contrast with the above results using zero lag, cross correlations between Bristol Bay and British Columbia sockeye ocean abundances at various lags show significant correlations at lags +2 and −3 yr. In the +2-yr case there is a large positive correlation of 0.77 between British Columbia age 2 abundances and those of Bristol Bay 2 yr later (n at that lag = 15, SE_{cr} = 0.292, $p = 0.021$). For age 5 fish, the significant case is at a lag of −3 yr, and there is thus a correlation of 0.834 between Bristol Bay abundances in year t and British Columbia abundances 3 yr later ($n = 16$, $SE_{cr} = 0.328$, $P = 0.024$). If we test the cross correlations assuming as in the previous paragraph that there is no autocorrelation above lag 5, then still only these same two age categories and lags are significant ($P < 0.02$). Further insight concerning lags can be obtained by examining the aggregate of signs of the cross correlations across age categories for each lag, regardless of the level of significance (Table 3). This cumulative information on signs of relations is a commonly used source of additional information (e.g. Ricker 1982). While noting that the bottom four age categories (2 + 3, 4 + 5, etc.) are not independent of the top five (age 2, 3, 4, 5, or 6), it is clear that negative correlations predominate at lags ±5, ±4, and 0 and positive ones at ±2 and ±3. Taking this evidence from the signs of the cross correlations together with the two significant cases noted above, there appears to be a 2- to 3-yr lag in fluctuations of Bristol Bay and British Columbia sockeye abundances in the ocean. The biological significance of these lags is discussed below.

Discussion

The cases of significant correlation between British Columbia and Bristol Bay abundances at several lags, including zero lag, suggest some form of interaction among these fish or an influence on them by some third variable. Possible explanations are discussed below in the context of another important feature of the data, lack of synchrony. Time series plots of ocean abundances illustrate that the British Columbia and Bristol Bay abundance cycles have remained out of synchrony throughout the whole 15- to 20-yr period covered in this study. See particularly Fig. 3g–3i. Yet because of the well-known differences in cyclic dominance patterns of British Columbia and

Bristol Bay stocks, their cycles should have shown evidence of drifting into synchrony during that period. This is because cyclic dominance generates a 4-yr cycle for the abundant Fraser River, B.C., stocks (Ward and Larkin 1964) and mainly a 5-yr cycle for the major Bristol Bay stocks (Mathisen and Poe 1981; Poe et al. 1977). In addition, from the data analyzed here the mean age at maturity averaged over all British Columbia stocks is roughly 4.2 yr and 5.0 yr for Bristol Bay stocks, so we would expect the peaks in abundances to coincide every $4 \times 5 = 20$ to $4.2 \times 5 = 21$ yr. The British Columbia and Bristol Bay abundances start the 1956–76 period out of synchrony, so if the cycles were completely independent, they should have drifted together roughly 10 yr later, but there is no evidence in the graphs of this occurring.

Several possible mechanisms can be hypothesized as causes of the failure of the two abundance cycles to drift into synchrony. First, the processes that set the period in one or both of the major cyclic dominant populations may have changed. Current understanding of the predator–prey dynamics that can give rise to cyclic dominance (Ward and Larkin 1964; Larkin 1971) does not indicate marine influences; i.e. most governing events probably occur in freshwater. Thus, if any event has caused an adjustment of one or both cycle frequencies to the point where the cycles are kept out of phase, the observed lack of synchrony in ocean abundances of British Columbia and Bristol Bay sockeye may merely be a coincidental result of independent freshwater processes. However, such a coincidental change is unlikely. Another freshwater phenomenon that can affect abundance patterns is a change in the age of smolting and its subsequent effect on age at maturity. Kvichak River sockeye smolts temporarily changed from mostly age 3 to mostly age 2 smolts in brood years 1952 and 1956, and most of the resulting adults matured at age 4 instead of the usual age 5 (Mathisen and Poe 1981). However, this change in age at maturity only affects the first part of our time series; the failure of British Columbia and Bristol Bay sockeye abundances to drift together during the last 10 yr of our time series is not explained by this observation. Investigation of more recent data is warranted and underscores the need for complete age structure data for British Columbia sockeye since 1973.

Second, the heavy harvesting that occurs on sockeye populations could have a large effect on abundance cycles, and the net result could be an adjustment of cycle times. However, most salmon managers attempt to maintain the basic sockeye cyclic dominance patterns in Bristol Bay and some British Columbia sockeye stocks by appropriate manipulation of harvests and escapements (IPSFC 1966; C. P. Meacham, pers. comm.; J. Woodey, IPSFC, pers. comm.). This management goal would tend to keep the cycles near their natural frequencies and we would therefore still expect that the abundance cycles should have drifted together by the mid- to late-1960s. Most British Columbia sockeye stocks, however, do not show clear cyclic dominance patterns, and therefore, British Columbia salmon managers may be inadvertently helping to keep the British Columbia and Bristol Bay sockeye abundance cycles out of phase through their management practices. However, this explanation is unlikely because the odds are low that management effects would have become large in the mid-1960s, at just the right time to keep the cycles from drifting together.

Third, oceanographic factors may influence sockeye abundances and thereby keep the British Columbia and Bristol Bay cycles apart. It is well known that fish generally are greatly affected by both physical and biological oceanographic variables (see Lasker 1978 and Cushing 1982 for reviews). Attributes of salmon populations such as survival, growth, and recruitment have been correlated with variables such as temperature and physical oceanographic features measured at locations distant from the fish-rearing areas (W. P. Wickett, DFO, Nanaimo, pers. comm.; IPSFC 1978), but the causal mechanisms remain unclear. For example, Mysak et al. (1982) showed in time series analyses that mean weight deviations from average weight for Fraser River sockeye are highly coherent with temperatures on the west coast of Vancouver Island 3–3.5 yr earlier. However, Fraser River sockeye go to sea at age 2 and mature mainly at age 4, so these results show either that (1) sea surface temperature reflects factors that affect eggs or fry in freshwater at that time or (2) the temperature reflects ocean conditions that are encountered by fish in *later* years when they are in salt water. But if the second were true, Mysak et al. (1982) should have found significant examples of those later temperature effects. Another difficulty with the oceanographic effects explanation of lagged cycles of British Columbia and Bristol Bay abundances is that survival of sockeye from those two regions would have to be affected in opposite directions. What little hard statistical evidence there is shows that survival rates of different salmon stocks that share common ocean entry years tend to fluctuate in the same direction, not the opposite. Godfrey (1958) found this for his indirect indices of rate of return for British Columbia pink (*Oncorhynchus gorbuscha*) and sockeye stocks, and Peterman (1978) found that the only examples of significant correlation among marine survival rates of British Columbia and Bristol Bay salmon stocks were positive. However, no significant correlations were found between British Columbia sockeye and Bristol Bay sockeye survival rates. So it is unlikely that oceanographic factors explain the out-of-phase abundance cycles either. The only example for which British Columbia and Bristol Bay sockeye are affected differently deals with seasonal run timings of sockeye stocks, not survival (IPSFC 1981; Killick and Clemens 1963; J. Woodey and D. J. Blackbourn, IPSFC, pers. comm.). Cooler sea temperatures displace both British Columbia and Bristol Bay sockeye southward in the Gulf of Alaska. This apparently causes Bristol Bay stocks to return later than usual to their home streams because of the greater travel distance involved, and some British Columbia stocks to return earlier. Another unexplored possibility of this type is that oceanographic changes that occur only in the southeastern part of the Gulf of Alaska may affect abundance of British Columbia stocks but not Bristol Bay stocks (Fig. 1), and similarly for oceanographic changes in the western edge of the Bristol Bay sockeye distribution where British Columbia sockeye are not found. Such phenomena could conceivably result in opposite patterns of sockeye abundance but the oceanographic changes would have to show periods of about 4–5 yr.

Fourth, indirect biological interactions may exist among sockeye in the Gulf of Alaska, since the distribution of British Columbia and Bristol Bay fish overlap in space and time (Fig. 1). These indirect interactions may be mediated through food supply, predator populations, or diseases. Changes in growth, survival, or mean age at maturity may be caused by large abundances of sockeye in the Gulf of Alaska, which may affect cycles in abundances of constituent stocks. Rogers (1980) is one of the few to have examined data relating sockeye sizes to abundance, and he found an inverse relation between adult body size of given ages and total returns to Bristol Bay in that year. He attributes these results to density-dependent growth in the

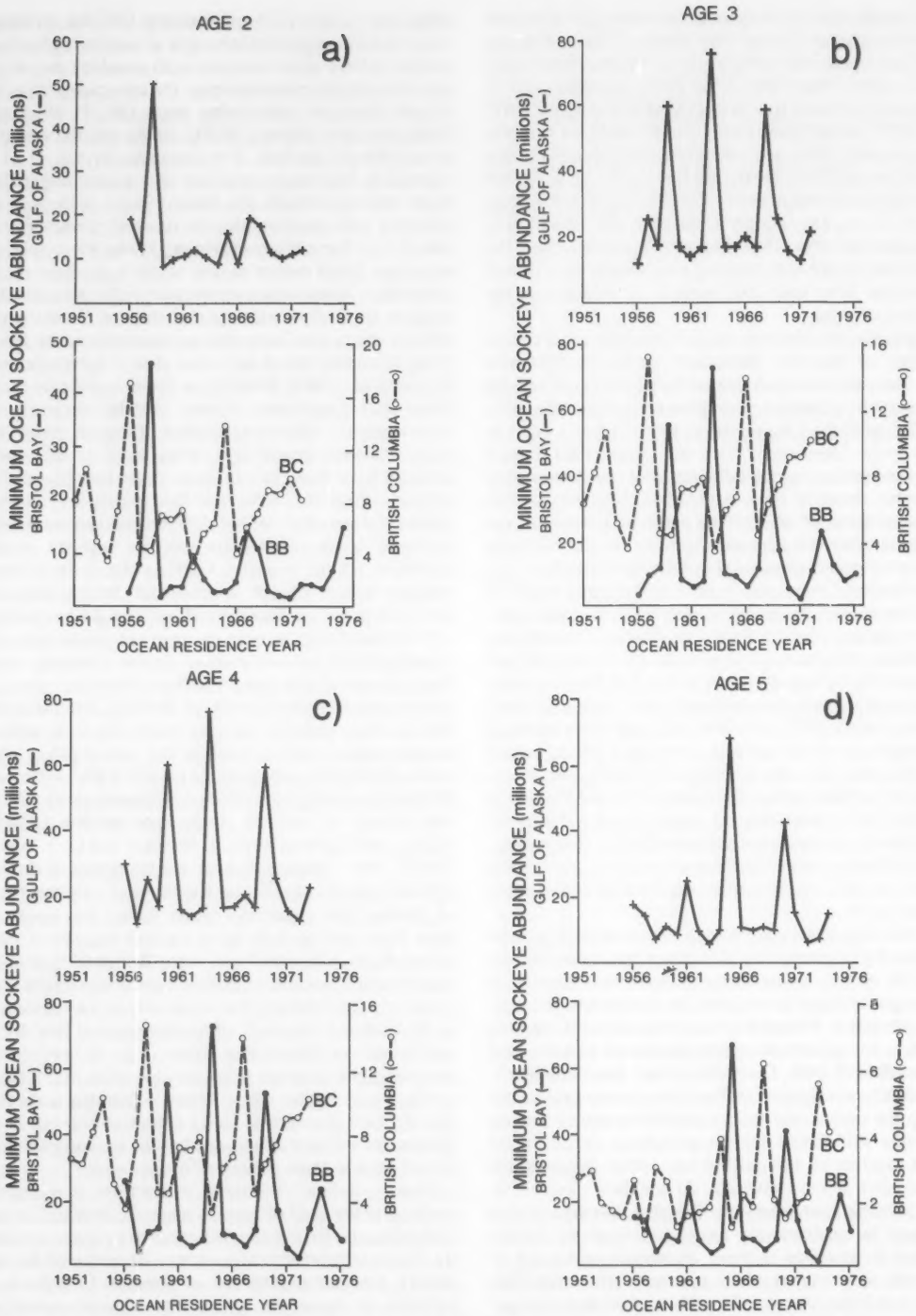

FIG. 3. Reconstructed minimum abundances of sockeye salmon of various ages that are resident in the Gulf of Alaska by ocean residence year. Bottom graph in each part shows abundances of sockeye of Bristol Bay origin (●) and of British Columbia origin (○). Note the different *y*-axis scales for these two populations. Top graph in each part shows total Gulf of Alaska abundance (which is the sum of the two abundances in lower half of the figure). (a) Age 2 abundances; (b) age 3 abundances; (c) age 4 abundances; (d) age 5 abundances; (e) age 6 abundances; (f) ages 2 + 3 abundances; (g) ages 4 + 5 abundances; (h) ages >2 abundances; (i) abundance of all ages.

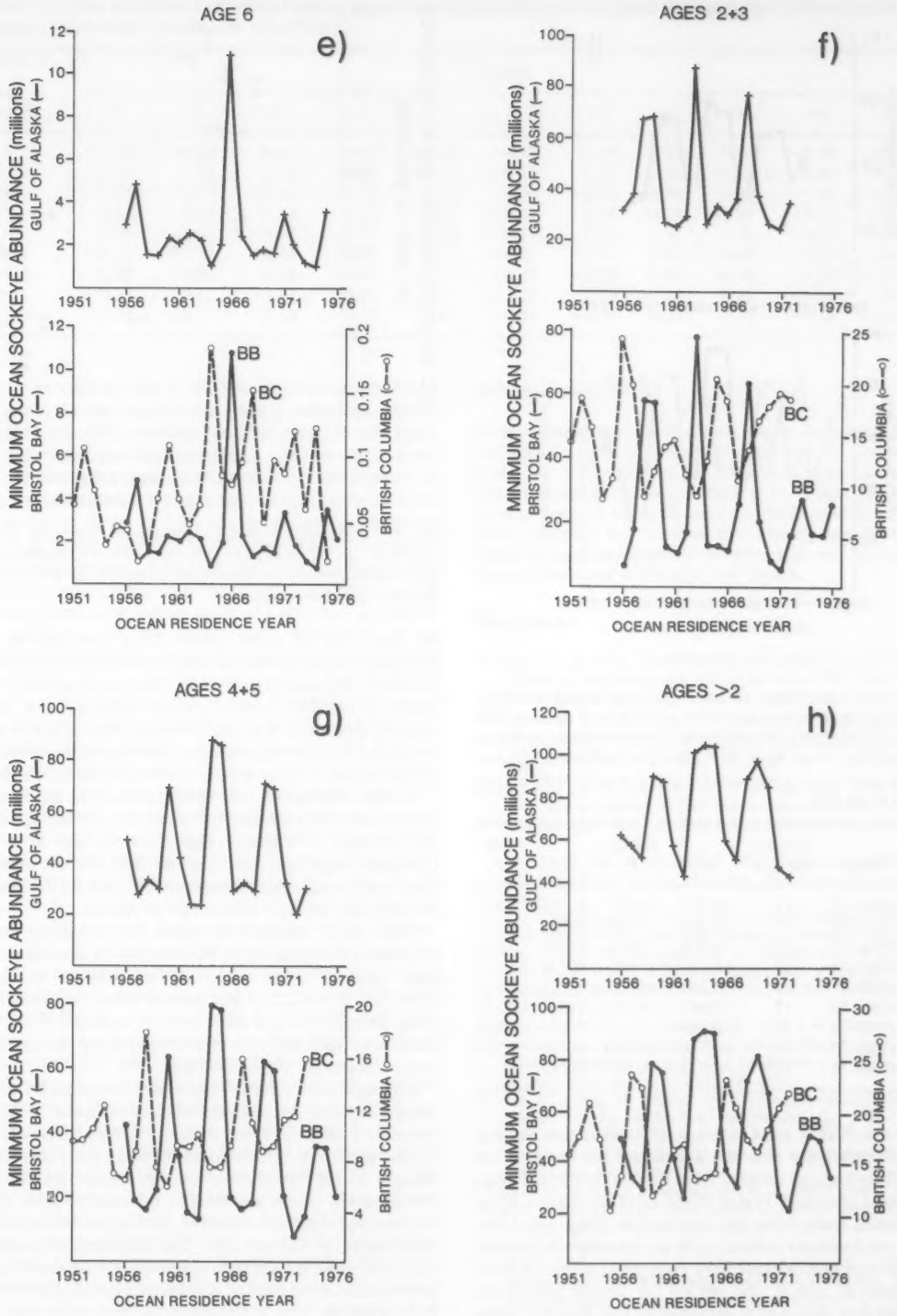

FIG. 3. (*Continued*)

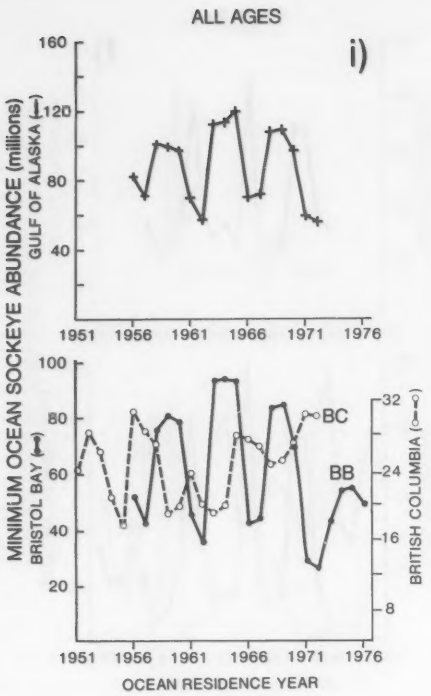

FIG. 3. (*Concluded*)

TABLE 2. Cross correlations between minimum British Columbia and Bristol Bay sockeye abundances in the ocean, at zero lag. Unadjusted *P* represents the probability in the standard method for testing the null hypothesis $r = 0$. Adjusted *P* represents that probability after the standard error of *r* is adjusted (SE_{cr}) for autocorrelation using equation (3) in the text.

Age category	Years	Sample size (yr)	*r*	Unadj. *P*	SE_{cr}	Adj. *P*
2	1956–72	17	−0.377	>0.05	0.255	>0.1
3	1956–72	17	−0.489	0.048	0.294	>0.1
4	1956–73	18	−0.499	0.04	0.295	>0.1
5	1956–74	19	−0.392	>0.05	0.278	>0.2
6	1956–75	20	−0.269	>0.05	0.217	>0.2
2 + 3	1956–72	17	−0.667	<0.01	0.319	>0.05
4 + 5	1956–73	18	−0.569	0.017	0.313	>0.1
>2	1956–72	17	−0.766	<0.001	0.326	>0.05
All ages	1956–72	17	−0.518	0.039	0.287	>0.1

last year at sea. Killick and Clemens (1963) also examined this question of adult body size and abundance for Fraser River sockeye. Their findings differed from Rogers' in that the years with the most abundant Fraser River catches (Adams River stock dominant runs) have the largest fish. They noted that stocks that are dominant in those years are inherently larger than other stocks and that because very large percentages of these adults mature at age 4, the stocks are almost genetically isolated. But data shown here demonstrate that British Columbia sockeye abundances, of which a large fraction come from the Fraser River, tend to be high in the Gulf of Alaska when total Gulf abundances are low. Thus, an alternative explanation of

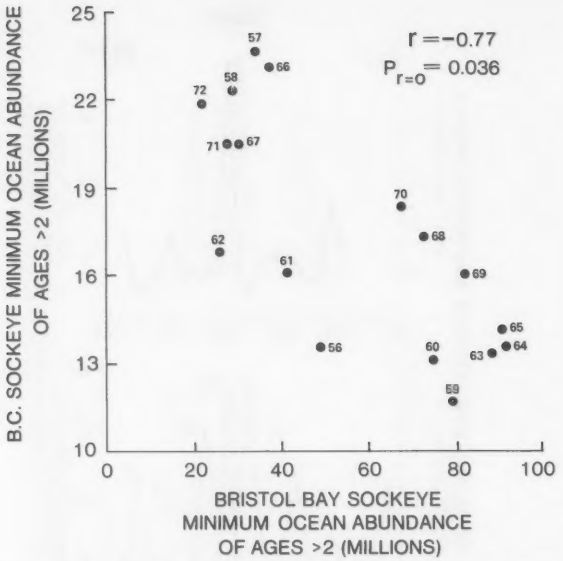
r = −0.77
P r=0 = 0.036
B.C. SOCKEYE MINIMUM OCEAN ABUNDANCE OF AGES >2 (MILLIONS)
BRISTOL BAY SOCKEYE MINIMUM OCEAN ABUNDANCE OF AGES >2 (MILLIONS)

FIG. 4. Correlation between reconstructed minimum ocean abundances of age >2 sockeye salmon from British Columbia and Bristol Bay. Probability shown reflects the correction for autocorrelation in the time series (see text).

the large size of some Fraser River fish may be density-dependent marine growth or differential effects of size-selective mortality. Because extensive data are now available for several stocks on variables such as growth, survival rates, and age at maturity that might potentially reflect some effect of total Gulf of Alaska sockeye abundances, this fourth hypothesis is explored further in other papers (Peterman 1984a, 1984b).

A fifth alternative, that British Columbia and Bristol Bay sockeye are being affected differently by interactions with other fish species, is virtually impossible to test at this point. Complete long-term age structure data are not available for other species that might reasonably be expected to compete with or prey upon sockeye in the Gulf of Alaska.

Time series analysis is useful for revealing patterns of abundance and pointing in the direction of alternative explanations such as those noted above (Botsford et al. 1982). However, this method has limited value for actually testing those alternatives, and other types of approaches are therefore necessary. Such analyses of alternatives are discussed in other papers (Peterman 1984a, 1984b).

Although total returns (catch plus escapement) of sockeye salmon are only an indirect indicator of ocean sockeye abundances in years prior to fish maturation, the anecdotally reported inverse pattern in British Columbia and Bristol Bay returns has brought to our attention a similar inverse relation between reconstructed ocean abundances of sockeye from those two regions, and significant positive correlations between those two abundances at various lags. The reconstructed ocean abundances of sockeye used here by age are a more direct estimate of fish resident in the Gulf of Alaska than annual total returns, but they represent only a minimum estimate. The lack of good survival data for most stocks and years precludes inflating those minimum estimates during the back-calculation process. If survival rates were available, the pattern of results described

TABLE 3. Cross correlation coefficients between reconstructed ocean abundances of Bristol Bay and British Columbia sockeye salmon at various lags. Sample sizes as in Table 2.

Age category	Lag (yr)										
	−5	−4	−3	−2	−1	0	+1	+2	+3	+4	+5
2	−0.16	−0.28	0.12	0.02	−0.02	−0.38	−0.22	0.77	0.05	−0.05	−0.11
3	−0.18	−0.27	0.52	0.08	−0.18	−0.49	−0.21	0.58	0.04	−0.26	−0.39
4	−0.17	−0.27	0.50	0.12	−0.17	−0.50	−0.15	0.58	0.08	−0.38	−0.34
5	−0.26	−0.04	0.83	−0.10	−0.20	−0.39	0.18	0.28	−0.01	−0.22	−0.32
6	−0.04	−0.05	−0.12	0.29	0.02	−0.27	0.02	0.47	0.01	−0.23	−0.09
2 + 3	−0.31	−0.32	0.22	0.37	−0.22	−0.67	−0.31	0.51	0.44	−0.20	−0.47
4 + 5	−0.29	−0.05	0.48	0.37	−0.29	−0.57	−0.19	0.48	0.20	−0.39	−0.50
>2	−0.24	−0.12	0.42	0.44	−0.11	−0.77	−0.28	0.42	0.17	−0.46	−0.46
All ages	−0.15	−0.17	0.18	0.37	−0.07	−0.52	−0.53	0.05	0.18	−0.16	−0.45

here would be altered only if the two populations exhibited different survival rates. Any factors tending to decrease marine survival rate (proportion surviving) of the most abundant stock more than the least abundant stock (e.g. due to within-stock effects) would tend to *increase* the current divergence in reconstructed abundances, which in turn would move the cross correlations closer to −1.0. This conclusion follows from the appearance of the survival rate in the denominator of equation (2), which would be used in the backwards stock reconstruction if survival rates were available. In the case stated above in which the most abundant stock suffers more of a decrease in survival than the smallest stock, the reconstructed abundances of the large stock would be increased more than those of the smallest stock. In contrast, factors tending to decrease marine survival of the Bristol Bay fish less than the British Columbia fish would tend to pull abundances closer together, pulling r closer to 0. Nothing in the current literature suggests that Bristol Bay and British Columbia sockeye survival rates fluctuate in opposite directions in any year. As noted above, they in fact tend to be positively correlated and fish from those two regions are approximately the same size at a given age and feed on similar organisms. Ocean abundances in this paper are given in number of fish rather than weight because total biomass requires not only size data by age but also age-specific survival rates for inflating abundances in the backwards reconstruction process. Given this lack of more complete data, then, the minimum ocean abundances shown here are used as the current best estimator of true abundances of sockeye salmon. While other salmon species beside sockeye reside in the Gulf of Alaska, abundance data are more incomplete for those species and it is difficult to extend this analysis to include them.

Several management implications arise from the observations on minimum ocean abundances of sockeye salmon in the Gulf of Alaska. There is a need for British Columbia and Bristol Bay fishery personnel to coordinate research and management activities, particularly if plans are carried out to "fill in" low abundance Bristol Bay years by increasing off-cycle escapements (C. P. Meacham, pers. comm.). More than just Bristol Bay fish might be affected if there are indirect interactions among stocks, as hypothesized by the fourth explanation discussed above. Similarly, plans to expand salmonid enhancement projects may have broader effects than recognized in earlier cost/benefit studies. These and other management implications are covered more extensively in another paper (Peterman 1984a).

Acknowledgments

We are extremely grateful to several people who made the initial data available: C. P. Meacham, A. D. Anderson, M. Farwell, and E. Zyblut. H. Stiff performed the backwards reconstruction of ocean abundances and R. Routledge steered us in the right direction on time series analysis. G. Geen, D. Ware, G. Hopky, and the referees made useful comments on the manuscript. Funding was provided by the Natural Sciences and Engineering Research Council of Canada and the Canada Department of Fisheries and Oceans.

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NOTES

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Randall M. Peterman

Natural Resource Management Program, Simon Fraser University, Burnaby, B.C. V5A 1S6

Peterman, R. M. 1984. Density-dependent growth in early ocean life of sockeye salmon (*Oncorhynchus nerka*). Can. J. Fish. Aquat. Sci. 41: 1825–1829.

Significant decreases in adult body size and marine growth rate occur in seven British Columbia and Bristol Bay, Alaska, sockeye salmon (*Oncorhynchus nerka*) stocks when large numbers of sockeye are present in the Gulf of Alaska. These density-dependent effects arise mainly during early ocean life and are probably due to competition for food. The total sockeye abundance in the Gulf of Alaska is at least as important as within-stock abundance in determining final adult body size. British Columbia sockeye show a 10–22% decrease in adult body weight at high abundance of conspecifics. Thus, future evaluations of management strategies cannot simply focus on individual stocks, but must take a broader perspective which includes other sockeye populations.

On a constaté qu'il se produit une baisse significative de la taille des adultes et du taux de croissance en mer dans sept stocks de saumon nerka (*Oncorhynchus nerka*) de la Colombie-Britannique et de la baie Bristol (Alaska), lorsqu'il y a un grand nombre de saumons de cette espèce dans le golfe de l'Alaska. Ces phénomènes sont liés à la densité des populations et se produisent principalement au début du cycle en mer ; ils sont probablement dus à la compétition que se font les poissons pour leur nourriture. L'effet de l'abondance totale du saumon nerka dans le golfe de l'Alaska sur la taille finale de l'adulte est aussi important, sinon plus, que celui de l'abondance d'un stock pris séparément. En Colombie-Britannique, lorsque le saumon nerka est abondant, le poids de l'adulte baisse de 10 à 22 %. Dans ce contexte, on ne peut plus concevoir les plans d'aménagement simplement en fonction de quelques stocks ; il faut adopter une perspective élargie et tenir compte d'autres populations de saumons.

Received February 23, 1984
Accepted August 17, 1984
(J7702)

Reçu le 23 février 1984
Accepté le 17 août 1984

Density-dependent growth or survival has been well documented for the freshwater life phase of Pacific salmon (*Oncorhynchus* spp.) (e.g. Foerster 1968 for review; Hunter 1959). In contrast, the marine life phase has received less scrutiny for density-dependent effects. Some papers have suggested that density dependence may exist in the ocean (e.g. Davidson and Vaughan 1941; Rogers 1980; Peterman 1982a); however, only incomplete estimates of salmon abundance in the ocean were used (e.g. catches only).

In this paper I test the hypothesis that characteristics of sockeye salmon (*O. nerka*) stocks such as marine growth or survival are density dependent. My analysis is based on more complete estimates of high seas sockeye abundance and a larger data set than used previously. Furthermore, I have been able to identify which segment of the marine life phase of sockeye is most important for density effects. For a detailed explanation of the analyses used in this study, see Peterman (1984).

Sockeye biology — Sockeye salmon from British Columbia and Bristol Bay, Alaska, rivers usually migrate to salt water during their 2nd or 3rd yr of life (called sub-2 or sub-3 fish). They spend about 2–3 yr in the Gulf of Alaska before returning to natal streams as mature adults aged 4–6 yr (Foerster 1968). Thus, fish that migrate seaward during their 2nd yr and mature during their 4th yr are designated as age 4_2. Sockeye from British Columbia and Bristol Bay comprise about 80% of the sockeye in the Gulf of Alaska (Fredin et al. 1977), and these two groups of stocks overlap considerably in both time and space (French et al. 1976).

Methods

Data — I reconstructed, by age, the abundance of British Columbia and Bristol Bay sockeye salmon which were resident in the Gulf of Alaska from the early 1950s to the mid-1970s. These high seas abundances were calculated by applying virtual population analysis to catch and escapement data (Peterman and Wong 1984). The total ocean abundances (of British Columbia plus Bristol Bay sockeye) were estimated for four segments of a typical salmon's ocean residence: ocean entry year (OEY),

ocean entry year + 1 (OEY + 1), OEY + 2, and OEY + 3. The OEY period of ocean residence corresponds to the first 4 mo of ocean life, and each of the next segments (OEY + 1, etc.) covers an additional 12 mo of ocean life. Ocean abundances of individual sockeye stocks were reconstructed using the same methods as for total ocean abundance. This resulted in two measures of sockeye abundance in the Gulf of Alaska: the within-stock abundance of certain stocks and the total abundance of all British Columbia and Bristol Bay stocks. Both measures were available by age category and for each ocean residence period.

Dependent variates used in the tests for density dependence were marine survival rate, residuals in marine survival rate from the best-fit smolt-to-adult relation (Peterman 1981), adult body size at a given age, smolt-to-adult growth rate, and weighted mean age at maturity for the brood class. Subsets of these data exist for each of 6 British Columbia and 10 Bristol Bay sockeye stocks (Peterman 1984). Because of lack of data on sub-3 populations in British Columbia, only sub-2 populations of British Columbia stocks were examined (Adams and Stellako rivers, Babine, Chilko, Cultus, and Owikeno lakes), but both sub-2 and sub-3 populations were included in the Bristol Bay stocks (Branch, Egegik, Igushik, Kvichak, Naknek, Nuyakuk, Snake, Togiak, Ugashik, and Wood rivers). Dependent variate data were available by sex for some stocks and were used preferentially over sexes-combined data.

Analysis — I used the within-stock and total stock abundances in multiple regression analyses to test whether density dependence exists in the dependent variables. I used the following multiple regression equation:

$$(1) \quad Y = a + b_1X_1 + b_2X_2$$

where Y = the dependent variables (marine survival and growth rates, adult body size, and age at maturity), X_1 = within-stock ocean abundance, and X_2 = total ocean abundance (British Columbia plus Bristol Bay stocks). I tested the null hypothesis that $b_2 = 0$ to determine whether there are significant density-dependent effects of total Gulf of Alaska sockeye abundance (X_2) in the presence of any potential effects of within-stock abundance (X_1). The latter variable was essential because of the previously mentioned prevalence of density-dependent effects within stocks. I did not know a priori in which period of ocean residence the total Gulf of Alaska abundance might be most important, nor which age categories of that abundance might be most significantly related to the dependent variates. So for each dependent variate of a given stock, such as size of age 4_2 adults, the multiple regression was repeated using X_1 and X_2 abundances for each age category and for each of the relevant ocean residence periods (OEY, OEY + 1, etc.). All analyses used $\alpha = 0.05$. As discussed in Peterman (1984), results were not influenced by the lack of independence of X_1 and X_2.

In terms of density dependence, I defined the most critical ocean residence periods and age categories of total Gulf of Alaska abundance as those with the largest fraction of significant b_2 values (slopes on X_2). I focused only on those ocean residence and age categories in which there were more rejections of the null hypothesis than expected by chance alone (as calculated from the binomial distribution).

Results

Seven British Columbia and Bristol Bay sockeye salmon stocks showed significant decreases in adult body size and marine growth rate when numbers of young sockeye in the Gulf of Alaska increased. The most important ocean residence periods for this density-dependent effect were in early ocean life: OEY + 1 for British Columbia and Bristol Bay sub-2 fish and OEY for Bristol Bay sub-3 fish. In these critical ocean residence periods, the abundances of age 3 (for sub-3 cases) and ages 2 and 3 combined (for sub-2 cases) were the age categories of total Gulf of Alaska abundance (X_2) which resulted in density-dependent size relations that had the most consistent patterns in sign across stocks. In contrast with body size, marine survival rates and mean age at maturity showed very few significant relations with abundance in any ocean residence period or age category analysis.

Two extreme cases of how within-stock and total Gulf of Alaska sockeye abundances affect adult body size of British Columbia sockeye stocks are illustrated in Fig. 1 and 2. The regression plane in Fig. 1 refers to standard length of age 4_2 females on the Chilko Lake spawning grounds (results for males are almost identical), as it relates to the abundances of ages 2 and 3 that are present during OEY + 1, the most critical ocean residence period for this stock. Both b_1 and b_2 in the resulting equation are signifiantly different from zero ($P < 0.05$, $P < 0.01$, respectively). Thus, increased numbers of total Gulf of Alaska sockeye (X_2) present during months 5–16 of ocean life of Chilko Lake sockeye significantly decrease the final adult body size of fish in that stock. This analysis shows that this influence holds even when within-stock (X_1) effects are taken into account. Similarly, Fig. 2 shows the effect of ocean sockeye abundances of ages 2 and 3 during OEY + 1 on fork length of age 5_2 Babine Lake sockeye sampled from the commercial catch (sexes combined because of lack of sexes-separate data). The slope b_1 is not significant but b_2 is ($P > 0.5$, $P = 0.005$, respectively). Using the historically observed ranges of X_1 and X_2 abundances in each case, and converting the lengths calculated from the multiple regression equations into weights, Chilko Lake sockeye are reduced in weight by 22% from their highest values, and Babine Lake fish are reduced by 10% when sockeye abundances are high. Several other British Columbia and Bristol Bay sockeye stocks show this same large, negative influence of high seas sockeye abundance on body weight (Peterman 1984).

To compare the relative importance of within-stock and total Gulf of Alaska sockeye abundance on adult sizes, b_1 and b_2 were converted into standard deviation units, and I tested the null hypothesis that $b_1 = b_2$ with the method of Graybill (1976, p. 183). The results for all sub-2 stock cases in which total Gulf of Alaska abundance of young sockeye present during the "critical" ocean residence period of OEY + 1 significantly affected adult body size or smolt-to-adult growth rates are shown in Table 1 (Peterman 1984 for results for all residence periods and ages). With one exception, $|b_2| > |b_1|$, although only three cases showed b_2 to be significantly different from b_1 at $\alpha = 0.05$. Therefore, the effect of Gulf of Alaska abundance on adult body sizes is *at least as important* as within-stock abundance.

Standardized slopes of size on Gulf of Alaska abundances are strikingly similar among British Columbia stocks (Table 1). With the exception of the small sample case ($n = 4$) and a case ($n = 8$) that has an outlier point at high abundance, the British Columbia b_2 values are within 0.13 standard deviation units of one another. It is unlikely that these results are simply

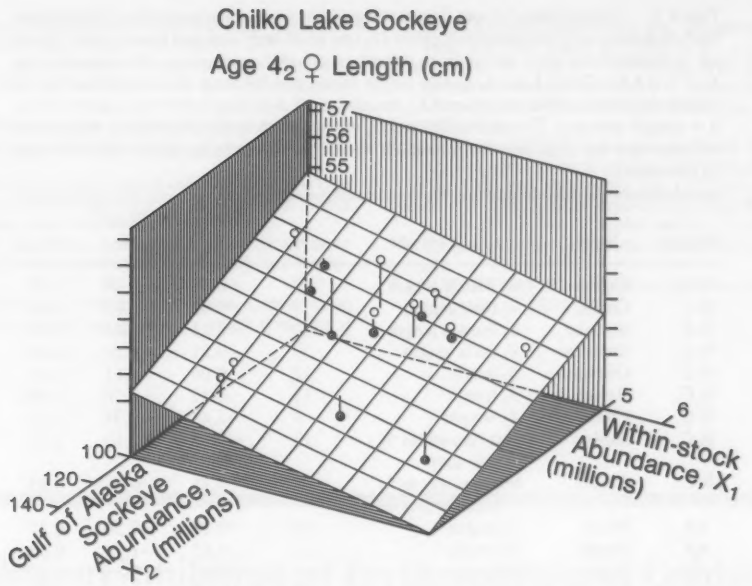

FIG. 1. Regression plane showing for Chilko Lake sockeye salmon the relation between ocean sockeye abundances and standard length of female age 4_2 fish. X_1 is ocean abundance of ages 2 and 3 Chilko Lake fish (within-stock abundance) and X_2 is the total ocean abundance of ages 2 and 3 sockeye summed across all British Columbia and Bristol Bay stocks (Gulf of Alaska sockeye abundance). Bottom back corner of the box is zero on both abundance axes and 49.6 cm on the size axis. The data ($n = 17$) are shown in relation to the regression plane by open circles (positive residuals) and solid circles (negative residuals). Multiple $r^2 = 0.46$, $Y = 54.8 - 0.46X_1 - 0.035X_2$.

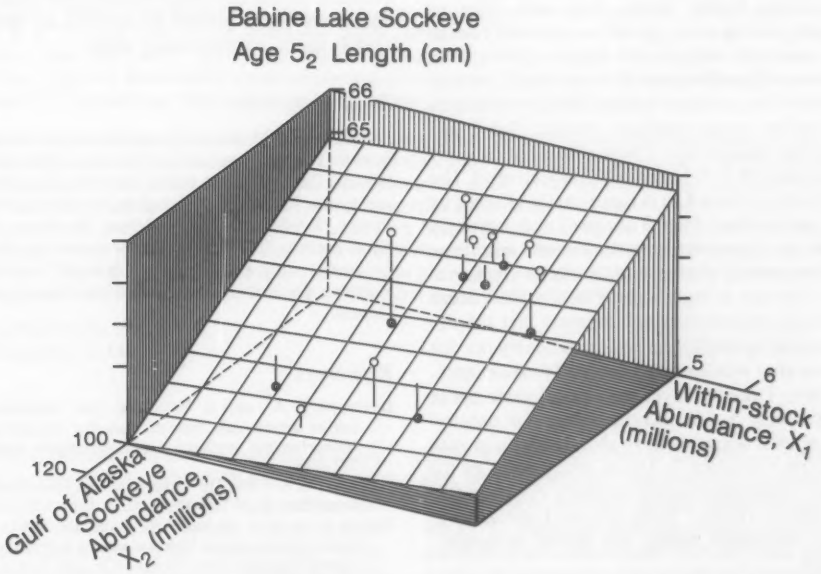

FIG. 2. Regression plane showing the relation between ocean abundances of ages 2 and 3 sockeye and fork length of age 5_2 Babine Lake sockeye salmon (sexes combined, $n = 15$). Multiple $r^2 = 0.56$, $Y = 64.9 + 0.14X_1 - 0.037X_2$.

TABLE 1. Comparison of slopes representing within-stock abundance effect (b_1) and total Gulf of Alaska sockeye abundance effect (b_2) on adult body size and growth rate. Slopes are in standard deviation (SD) units to permit meaningful comparisons. For example, the $b_2 = -0.6$ for Chilko Lake 4_2 female length means that for every SD unit of total Gulf of Alaska abundance above the mean of X_2, female length decreases below its mean by 0.6 SD. n = sample size (yr). The probability that $b_1 = b_2$ is given in the last column. An asterisk indicates that the slope may be influenced by one or two extreme outlier points at high X_2 abundance.

Region	Stock	Y variate	n	(Within) b_1	(Total) b_2	$P_{b_1=b_2}$
B.C.	Chilko	4_2 female length	17	−0.43	−0.60	0.55
B.C.	Chilko	4_2 male length	17	−0.43	−0.63	0.46
B.C.	Stellako	4_2 female length	17	−0.11	−0.61	0.09
B.C.	Stellako	4_2 male length	17	−0.21	−0.57	0.23
B.C.	Owikeno	5_2 length	15	0.06	−0.61	0.02
B.C.	Babine	5_2 length	15	0.10	−0.70	0.005
B.C.	Chilko	4_2 weight	4	−1.48	−1.35	0.28
B.C.	Babine	Inst. growth to 5_2 (gill net)	12	−0.35	−0.69	0.30
B.C.	Babine	Inst. growth to 5_2 females (test fishery)	8	−0.75	−0.78*	0.95
AK	Wood	5_2 length	15	−0.20	−0.56	0.37
AK	Egegik	5_2 length	17	0.65	−1.24	0.08
AK	Togiak	4_2 length	11	−0.80	0.85*	0.02
AK	Wood	3_2 length	7	−0.92	1.01*	0.74

collections of spurious relations because such close resemblance among different stocks is highly improbable by chance alone.

Discussion

These results show that sockeye salmon exhibit density-dependent growth in the ocean (as do numerous other marine fish species, Ware 1980). My analysis of all periods of marine life of sockeye salmon further shows that most cases of significant density-dependent ocean growth occur in early ocean life. This finding contrasts with that of Rogers (1980), who concluded that density-dependent growth occurs in the last year of ocean life of Bristol Bay sockeye salmon. However, Rogers did not examine earlier ocean residence periods. Sub-2 and sub-3 fish are either late age 2 or age 3 during their critical early ocean residence periods (OEY + 1 and OEY, respectively). The observation that growth of these fish is significantly affected by the abundance of conspecifics of age 3 or ages 2 and 3 strongly suggest that the density-dependent growth relations arise from competition for food among similar-sized sockeye (Peterman 1984). In addition, the lack of significant effects of total ocean sockeye abundance on marine survival suggests that the observed density-dependent growth relations are probably not due to size-selective mortality which might be related to abundance. In the case of Babine Lake sockeye, the critical early ocean residence period (months 5–16) identified here for density-dependent effects of total ocean sockeye abundance on growth is similar to the period (months 0–15) in which most of the within-stock density-dependent marine mortality occurs in that stock (Peterman 1982a, 1982b). Thus, Babine Lake sockeye appear particularly vulnerable during that period to density-dependent processes.

Within-stock and total ocean sockeye abundances explain an average of 54% of the variability in sockeye adult body size or growth rates for the 13 cases listed in Table 1. The remaining variation in size may be due to ocean temperature effects (Killick and Clemens 1963; Ricker 1982), or effects of abundance of other fish species such as pink (*O. gorbuscha*) and chum salmon (*O. keta*), which feed on some of the same prey types as sockeye salmon.

The large effects of Gulf of Alaska sockeye abundance on adult size, and hence on fecundity and weight of catches, suggest that evaluations of sockeye management strategies cannot focus simply on individual stocks; broader methods are essential. These and other management implications of density-dependent ocean growth of sockeye are detailed in Peterman (1984) and in a forthcoming paper.

Acknowledgments

Assistance with this study was kindly provided by numerous people from the Alaska Department of Fisheries, Department of Fisheries and Oceans (Canada), International Pacific Salmon Fisheries Commission, and Simon Fraser University (detailed names in Peterman 1984). Bill Ricker, T. Nickelson, J. Anderson, G. Steer, and especially Mart Gross made useful comments on the manuscript. Funding was provided by an operating grant from the Natural Sciences and Engineering Research Council of Canada and the Department of Fisheries and Oceans.

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Cadmium Inhibition of Erythropoiesis in Goldfish, *Carassius auratus*

A. H. Houston and J. E. Keen

Department of Biological Sciences, Brock University, St. Catharines, Ont. L2S 3A1

Houston, A. H., and J. E. Keen. 1984. Cadmium inhibition of erythropoiesis in goldfish, *Carassius auratus*. Can. J. Fish. Aquat. Sci. 41: 1829–1834.

Goldfish (*Carassius auratus*) maintained on a highly nutritional diet under normoxic circumstances at 25°C in soft water had mean half-recovery times of 22.5 h (hemoglobin) and 21.0 h (hematocrit) following anemia induced with phenylhydrazine HCl. Corresponding values for fish exposed under similar conditions to 1, 5, 15, and 25% of the softwater 240-h cadmium LC50 were 41.9, 53.1, 164.8, and 344.3 h (hemoglobin) and 44.7, 46.5, 348.9, and 263.2 h (hematocrit), respectively. We suggest that whereas cadmium has relatively little effect upon circulating erythrocytes, it seriously impedes red cell formation and hemoglobin synthesis at concentrations well below the acutely lethal level.

Chez le poisson doré (*Carassius auratus*) anémié par administration de chlorhydrate de phénylhydrazine, soumis à un régime hautement nutritif et gardé en eau douce en condition de normoxie à 25°C, la période de semi-récupération moyenne est de 22,5 h (hémoglobine) et de 21,0 h (hématocrite). La valeur correspondante de la CL50 du cadmium chez les poissons gardés 240 h dans les mêmes conditions dans 1,5, 15 et 25 % d'eau douce était de 41,9, 53,1, 164,8 et 344,3 h (hémoglobine) et de 44,7, 46,5, 348,9 et 263,2 h, respectivement. Nous pensons que le cadmium a relativement peu d'effets sur les érythrocytes en circulation, mais qu'il peut gravement nuire à la formation des globules rouges et à la synthèse de l'hémoglobine à une concentration de beaucoup inférieure à celle où il a des effets létaux aigus.

Received October 31, 1983
Accepted August 13, 1984
(J7597)

Reçu le 31 octobre 1983
Accepté le 13 août 1984

Histological and biochemical studies, as well as tissue analysis (Gardner and Yevich 1970; Ohmono et al. 1972; Clearley and Coleman 1974; Newman and MacLean 1974; Rowe and Massaro 1974; Larsson 1975; Tafanelli and Summerfelt 1975; Voyer et al. 1975; McCarty and Houston 1976; Sangalong and Freeman 1979; Stromberg et al. 1983), have demonstrated that marine and freshwater fishes readily take up cadmium, frequently at ambient concentrations well below lethal levels (Pickering and Henderson 1966; Pickering and Gast 1972; McCarty et al. 1978). Chronic exposure to sublethal concentrations is associated with significant, concentration-dependent reductions in blood oxygen-carrying capacity (Johansson-Sjobeck and Larsson 1978). Although cadmium effects tissue water content and distribution to some extent (McCarty and Houston 1976), the anemia observed cannot be attributed to persistent hemodilution (Larsson et al. 1976). Presumably, then, it is a consequence of impaired erythropoiesis and (or) accelerated erythrocytic breakdown. Our study addressed the former possibility through assessment of erythropoietic capacity in goldfish, *Carassius*

auratus, exposed for 14 d to cadmium concentrations ranging from 1 to 25% of a previously determined softwater LC50 for this species (McCarty et al. 1978).

Materials and Methods

Goldfish of both sexes ranging in weight from 5.0 to 20.9 g (mean ± 1 SD, 8.7 ± 0.6 g) were normoxically ($Po_2 \sim 80\%$ saturation) acclimated to near-optimal temperature conditions (25.0 ± 0.2°C) for at least 3 wk before use. A 12 h light : 12 h dark photoperiod regime was maintained throughout the study, and the fish were fed twice daily (09:00, 15:00) to satiation. Holding conditions were otherwise similar to those previously described (Koss and Houston 1981).

The cadmium content of St. Catharines city water is relatively low ($<10\ \mu g \cdot L^{-1}$), and zinc and copper concentrations are below levels ($<50\ \mu g \cdot L^{-1}$) that would be expected to influence cadmium toxicity. Total hardness (140–145 $mg \cdot L^{-1}$, as $CaCO_3$) and pH (7.6–8.0) are, however, such that added cadmium rapidly precipitates (McCarty et al. 1978). To avoid this, all tests were conducted in water of reduced hardness (20–22 $mg \cdot L^{-1}$, as $CaCO_3$) prepared as previously described (McCarty et al. 1978) by dilution of aged and dechlorinated city water with deionized, glass-distilled water. Under these circumstances, there is relatively little variation in water cadmium concentration with time, and the changes in total hardness, total alkalinity, and pH that follow cadmium addition are substantially reduced (McCarty et al. 1978). The cadmium content of water prepared in this way was $<2\ \mu g \cdot L^{-1}$.

Erythropoietic capacity was estimated in terms of recovery from induced anemia. Several methods (hemorrhage, starvation, blood withdrawal from implanted catheters, hypophysectomy) have been used to stimulate erythropoiesis in this way (e.g. Slicher and Pickford 1968; Weinberg et al. 1976; McLeod et al. 1978; Lane 1979). The hemolytic agent, phenylhydrazine HCl (Sigma grade crystalline), appears to offer a number of advantages over these (Cameron and Wohlschlag 1969; Smith et al. 1971). The effects are transient, with recovery taking place within a few days. No major side effects have been reported in fishes, and the widespread and persistent changes in hematology and body fluid composition and distribution that follow hemorrhage and the surgical manipulation of fishes are largely avoided (Houston et al. 1971). The handling stresses associated with administration by injection would, however, be expected to prompt some alteration in hematological status (Houston et al. 1969).

Three groups of fish were examined in initial trials carried out in "cadmium-free" water (i.e. $[Cd] < 2\ \mu g \cdot L^{-1}$). Of these, one was sampled regularly over the study period to assess "spontaneous" changes in hematological status as described by Denton and Yousef (1975). To examine the effects of handling stresses per se, we treated a second group with single intraperitoneal injections of phenylhydrazine-free sterile Cortland saline (Wolf 1963) following light anesthetization in freshly prepared, aqueous tricaine methane sulphonate (MS-222, 50 $mg \cdot L^{-1}$). These fish were sampled prior to treatment and 12, 18, 24, and 36 h after injection. A third group, similarly handled, was treated with phenylhydrazine at a dosage (15 $\mu g \cdot g$ body $weight^{-1}$ in sterile saline) that reduces hemoglobin levels by ~ 50% within 12–24 h (Chudzik and Houston 1983). Sampling was carried out immediately prior to treatment and following 12, 18, 24, 36, 48, 72, 96, 144, and 240 h of recovery. Three replicates were carried out, six or nine fish being sampled at each period.

Following completion of these trials, groups were exposed for 14 d to 18, 90, 270, and 445 $\mu g\ Cd \cdot L^{-1}$, concentrations equivalent to 1, 5, 15, and 25% of the 240-h LC50 for this species under comparable test conditions (McCarty et al. 1978). Groups of 10 fish were first taken to ascertain the effects of these exposures on hemoglobin and hematocrit. The remainder were injected with phenylhydrazine and sampled after 12, 18, 24, 36, 48, 72, and 96 h. Replicates were carried out to provide groups of 5 or 10 animals at each interval.

Sampling and analysis — Midwater samples were collected daily and cadmium determined using a Perkin-Elmer model 403 AAS, small amounts of cadmium or softened water being added as required to maintain concentrations. Blood samples were drawn by caudal vessel puncture or, in the case of small specimens after caudal transection, into ammonium heparin-treated syringes, and chilled on ice. Microhematocrit was immediately determined in the usual fashion, and hemoglobin as described by Anthony (1961).

Trend lines describing the induction of, and recovery from, anemia were best-fitted using maximum coefficient of determination as the criterion. Simple linear ($Y = a + bX$), power ($Y = aX^b$), exponential ($y = ae^{bX}$), and logarithmic ($Y = a + b \ln X$) functions were tested in each case. The points of intersection of induction and recovery curves were calculated, and maximum reductions in hemoglobin and hematocrit estimated by comparison with initial values. Taking these points as time zero for recovery, recovery curves were solved for the time required for restoration of one half of the maximum reduction. These half-recovery values have been used as indicators of erythropoietic capacity.

Descriptive statistics were estimated from untransformed data. Hemoglobin and hematocrit values for the various sample groups were tested for homogeniety of variance. These proved to be non-significant, and differences in group means were evaluated by *t*-tests, significance being attributed to differences at the 0.05 level or better.

Results and Discussion

Trials in cadmium-free water — The mean hemoglobin content of 48 untreated goldfish was 6.63 ± 0.25 $g \cdot dL^{-1}$, whole blood (mean ± 95% confidence interval of the mean) and hematocrit, 31.8 ± 1.58%, values comparable with those reported for this species under similar conditions (e.g. Anthony 1961; Koss and Houston 1981). No significant changes with time were observed, and this points to the absence of spontaneous variation over the study period.

Saline-injected fish exhibited transient but significant decreases in hemoglobin and hematocrit (Fig. 1). Minimum values were observed after 12 h, and recovery was essentially complete within 24 h. This stress-induced anemia, comparable in magnitude and duration with that reported for other species (e.g. Houston et al. 1969; Soivio et al. 1972), is thought to reflect changes in tissue water content and distribution rather than red cell destruction per se.

Phenylhydrazine treatment led to sharp reductions in hemoglobin and hematocrit (Fig. 1). Maximum effects were evident after 18 h and were roughly twice those observed following handling stress alone. Several specimens dissected at this time, as might be anticipated, exhibited gross enlargement of the spleen. Both indices increased steadily thereafter and by 96–144 h were comparable with those of untreated animals. Induction and recovery curves were best-fitted by logarithmic

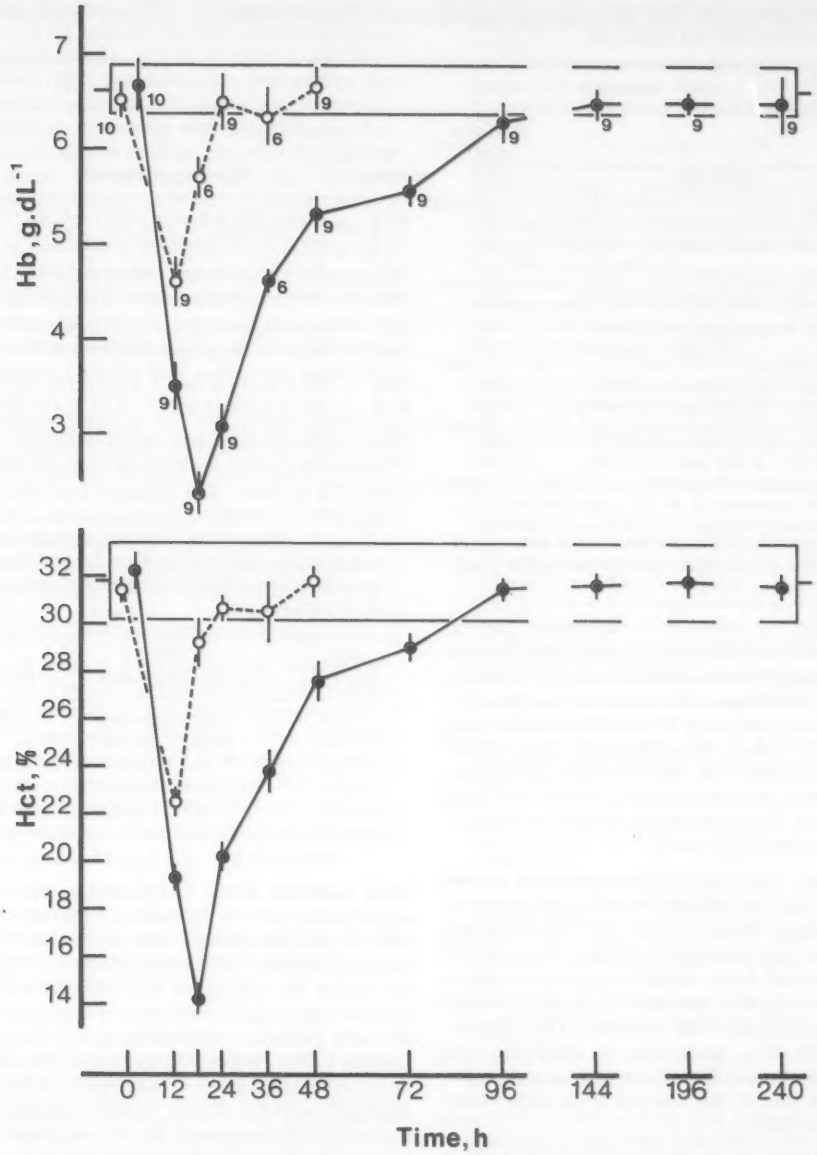

FIG. 1. Hemoglobin and hematocrit in untreated, saline-injected (○) and phenylhydrazine treated (●) goldfish. Hemoglobin and hematocrit in untreated fish did not vary significantly with time and are indicated as envelopes covering the mean ± 95% confidence interval of the mean. Vertical lines represent 95% confidence interval of the mean. Sample sizes as indicated.

functions (Table 1). For recovery, best fit was obtained using data from the 18- to 96-h sampling periods. Inclusion of values from the 144-, 199-, and 240-h samples weighted the curve, increasing intercept while reducing slope. Consequently, these values were not included in calculations. Estimated half-recovery times were 21.0 (hematocrit) and 22.5 h (hemoglobin).

Clearly, under the conditions we obtained, goldfish were capable of rapid erythropoietic recovery from phenylhydrazine-induced anemia. We considered response to be well regulated because both hematocrit and hemoglobin values converged on those characteristic of untreated fish without overshoot or oscillation. In this respect, our findings confirm earlier conclusions regarding the precision with which red cell production is controlled in this species (Chudzik and Houston 1983). The nature of the stimulus(i) triggering erythropoiesis cannot be inferred from the data obtained. However, by analogy with higher vertebrates, it seems reasonable to speculate that the hypoxia resulting from reduced oxygen-carrying capacity, or some consequent condition, prompts formation and release of an erythropoietin-

TABLE 1. Induction of and recovery from phenylhydrazine-induced anemia in goldfish exposed to cadmium (* significant at the 0.05 level; ** significant at the 0.01 level; NS, not significant).

	Induction			Recovery		
Cd ($\mu g \cdot L^{-1}$)	Induction	Maximum effect (h)	% reduction	Recovery relationship	Half-recovery (h)	96 h/ 0 h
<2	Hb = 4.05 − 0.381 ln time (r = −0.968**)	16	62.5	Hb = 2.205 ln time − 3.63 (r = 0.968**)	22.5	0.962
	Hct = 21.40 − 1.577 ln time (−0.957**)	15	53.2	Hct = 9.362 ln time − 9.36 (0.952**)	21.0	0.998
18	Hb = 7.46 − 0.350 time (−0.777**)	11	49.5	Hb = 1.468 ln time + 0.19 (0.554**)	41.9	0.873
	Hct = 31.74 − 1.243 time (−0.769**)	15	41.7	Hct = 4.116 ln time + 8.58 (0.420**)	44.7	0.867
90	Hb = 7.24 − 0.285 time (−0.911**)	11	47.2	Hb = 0.761 ln time + 2.38 (0.347*)	53.1	0.812
	Hct = 31.32 − 1.398 time (−0.909**)	11	50.2	Hct = 4.789 ln time + 4.07 (0.589**)	46.3	0.834
270	Hb = 7.60 − 0.174 time (−0.715**)	20	55.0	Hb = 0.398 ln time + 2.94 (0.145 NS)	164.8	0.628
	Hct = 36.06 − 0.834 time (−0.790**)	21	47.6	Hct = 2.130 ln time + 12.12 (0.171 NS)	348.9	0.608
445	Hb = 7.04 − 0.326 time (−0.967**)	11	55.6	Hb = 0.476 ln time + 2.29 (0.319*)	344.3	0.636
	Hct = 30.08 − 1.003 time (−0.682*)	11	46.8	Hct = 1.843 ln time + 14.19 (0.237 NS)	263.2	0.654

like hormone (Zanjani et al. 1969) and that this, in turn, stimulates red cell formation in the head kidney and other blood-forming regions.

Effects of exposure to cadmium — Untreated goldfish exposed for 14 d to sublethal cadmium concentrations exhibited some variation in hemoglobin and hematocrit levels (Table 2). Although significant differences were apparent in some comparisons, no consistent relationship between these indices and ambient cadmium was evident. We suggest that, at the concentrations employed, cadmium has little obvious effect upon circulating erythrocytes. Generally similar findings have been reported by Smith et al. (1976) for catfish, *Ictalurus punctatus*, exposed to cadmium for several weeks.

Induction of anemia — Possibly, cadmium influences red cell membrane structure, and the anemia observed subsequent to cadmium exposure stems, in part at least, from the accelerated breakdown of erythrocytes weakened in this way. If so, the red cells of cadmium-exposed fishes would be expected to hemolyze more rapidly and in greater numbers than those of control animals following phenylhydrazine treatment. Our observations mediate against this. Reductions in hematocrit and hemoglobin were not greater than those encountered in the control group and, in general, this was true of the slope values of induction curves as well.

Recovery from phenylhydrazine treatment — While both of these indices as well as rates of hemolysis following phenylhydrazine administration appeared to be insensitive to cadmium, this was not true of erythropoietic capacity. Recovery curves were best-fitted by logarithmic functions (Table 1). Decreases in the slopes were apparent at higher cadmium concentrations; this was also true of correlation coefficients. Consequently, values for half-recovery times increased, while extent of recovery, estimated as the ratio of 96-h to 0-h values, dropped sharply.

Although effects of the kind observed are consistent with cadmium-induced decreases in the hemolytic efficacy of phenylhydrazine, or with increases in its retention time, this seems unlikely. Stromberg et al. (1983) have, moreover, reported a high and persistent incidence of hemopoietic necrosis in fathead minnows, *Pimephales promelas*,transiently exposed to sublethal cadmium levels. Consequently, direct suppression of erythropoietic activity by cadmium provides a more plausible basis for our observations. The mechanism(s) responsible are, however, unclear. Unlike lead (Hodson 1976), cadmium does not inhibit the activity of δ-aminolevulinate dehydrase, the enzyme catalyzing condensation of δ-aminolevulinate to form the heme precursor, porphobilinogen (Johansson-Sjobeck and Larsson 1978). Prolonged exposure of flounder, *Pleuronectes flesus*, to sublethal levels of cadmium is, in fact, associated with increased activity of this system. Johansson-Sjobeck and Larsson (1978) interpreted this as compensatory response to a biochemical lesion or lesions introduced at later stages in hemoglobin formation. Studies on other vertebrates (e.g. Richardson et al. 1974) suggest cadmium impairment of some aspect of iron metabolism.

TABLE 2. Hemoglobin (Hb) and hematocrit (Hct) in goldfish exposed to sublethal cadmium for 14 d. Values reported as mean ± 95% confidence interval of the mean (sample size in parentheses).

Cd ($\mu g \cdot L^{-1}$)	Hb ($mg \cdot dL$ whole $blood^{-1}$)	Hct (% whole blood)
<2	6.63±0.25 (48)	31.8±1.58 (48)
18	7.56±0.40 (10)	31.7±2.43 (10)
90	7.24±0.29 (10)	31.3±1.94 (10)
270	7.54±0.33 (10)	35.8±2.56 (10)
445	7.04±0.33 (10)	30.1±3.96 (10)

We suggest from our study, and those cited (Smith et al. 1976; Johansson-Sjobeck and Larsson 1978; Stromberg et al 1983), that at sublethal concentrations, cadmium has little, if any, effect upon circulating red cells but a profound influence upon ability to form new cells. Some probable consequences of such erythropoietic suppression are readily inferred. For example, one aspect of response to temperature-induced increase in oxygen demand involves elevation of blood oxygen-carrying capacity: primarily through provision of a larger number of smaller erythrocytes of somewhat higher hemoglobin content (Houston 1980). Red cell life span appears to be an inverse function of temperature (Hevesy et al. 1964; Weinberg et al.

1976; Chudzik and Houston 1983). Compensation for inadequate oxygen-carrying capacity normally involves increases in ventilatory and (or) cardiac activity (Cameron and Davis 1970; Smith and Jones 1982). In combination, these factors may place fishes exposed to sublethal cadmium concentrations at severe risk when they are confronted with circumstances (e.g. the relatively rapid warming of shallow, slow-flowing habitats that takes place during the late spring and early summer) requiring increased respiratory activity. Although oxygen requirements rise, red cell life span is presumably reduced, while ability to form new cells is impaired. Since the gills are a principal avenue of cadmium uptake, compensatory increases in branchial ventilation and perfusion would be expected to elevate cadmium uptake rate, and further suppress erythropoiesis. In short, a form of positive feedback leading to profound reduction in oxygen-carrying capacity may well ensue under such circumstances.

Finally, observations made in this and earlier studies on chronic cadmium intoxification have some bearing on the question of maximum acceptable toxicant concentration (MATC) values. Whereas early investigations (e.g. Hart, et al. 1945) suggested that concentrations equal to 20–30% of LC50 might be acceptable over the long term, subsequent studies have invariably led to the recommendation of much lower values. In the specific instance of cadmium, Pickering and Gast (1972) suggested a MATC of 25–57 $\mu g\,Cd \cdot L^{-1}$ for fathead minnow in relatively hard water (201 ± 6.1 to $204 \pm 8.4\,mg \cdot L^{-1}$, as $CaCO_3$). Goldfish in water of somewhat lower total hardness (147 ± 4.5 to $152 \pm 5.2\,mg \cdot L^{-1}$) exhibited significant changes in water–electrolyte balance at cadmium concentrations as low as $44.5\,\mu g \cdot L^{-1}$ (McCarty and Houston 1976). Detectable hematological changes were observed in flounder exposed in brackish water (7.4‰) to cadmium concentrations of $\sim 5\,\mu g \cdot L^{-1}$ (Johansson-Sjobeck and Larsson 1978). Similarly, our study points to some impairment in erythropoietic capacity following relatively brief exposure to $18\,\mu g\,Cd \cdot L^{-1}$ in soft water.

Acknowledgments

We gratefully acknowledge the financial support provided by the Natural Sciences and Engineering Research Council of Canada through operating grant A6972 to A. H. Houston.

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Electrophoretic Identification of Atlantic Salmon (*Salmo salar*), Brown Trout (*S. trutta*), and Their Hybrids

Jukka Vuorinen and Jorma Piironen

Department of Biology, University of Joensuu, Box 111, SF-80101 Joensuu, Finland

Vuorinen, J., and J. Piironen. 1984. Electrophoretic identification of Atlantic salmon (*Salmo salar*), brown trout (*S. trutta*), and their hybrids. Can. J. Fish. Aquat. Sci. 41: 1834–1837.

We studied 14 enzyme systems of Atlantic salmon (*Salmo salar*), brown trout (*S. trutta*), and their F1 hybrids. Five enzymes, namely glucosephosphate isomerase, malic enzyme, phosphoglucomutase, superoxide dismutase, and xanthine dehydrogenase, were diagnostic in providing reliable separation of the species and their hybrids. The most anodal locus of glucosephosphate isomerase exhibited adequate activity also in adipose fin biopsies, thus allowing the identification of live fish.

Nous avons étudié 14 des systèmes enzymatiques du saumon atlantique (*Salmo salar*), de la truite brune (*S. trutta*) et de leurs hybrides de génération F1. Nous avons trouvé cinq enzymes permettant de distinguer de façon fiable ces deux espèces et leurs hybrides ; il s'agit de la glucosephosphate-isomérase, de l'enzyme malique, de la phosphoglucomutase, de la superoxyde-dismutase et de la xanthine-déshydrogénase. Comme l'activité du locus de la glucosephosphate-isomérase le plus près de l'anode est suffisante dans les tissus adipeux des nageoires, il est possible d'identifier les poissons vivants.

Received March 27, 1984
Accepted August 22, 1984
(J7742)

Reçu le 27 mars 1984
Accepté le 22 août 1984

Atlantic salmon (*Salmo salar*) and brown trout (*S. trutta*) are morphologically similar. Because most of their diagnostic characters overlap, separating these species on the basis of external characters is often difficult. This uncertainty is particularly a concern in juveniles, but persists in some cases in hatchery-reared adults. In spite of different chromosome numbers (salmon $2n = 58$, trout $2n = 80$; Nygren et al. 1975) these two species hybridize. In the wild, this is not extensive (Solomon and Child 1978; Beland et al. 1981). However, in hatcheries the hybrids are easily produced (Alm 1955; Piggins 1965; Refstie and Gjedrem 1975; Chevassus 1979) but their fertility is still the object of controversy (e.g. see Chevassus 1979). On the basis of conventional fish taxonomic characters the diagnosis of hybrids is highly uncertain: they have been reported to resemble salmon (Solomon and Child 1978) or trout (Piggins 1965; Payne et al. 1972). Accordingly, caution is necessary in fish-farming to avoid undesired hybridization.

Electrophoretic differences between salmon and trout were first found in esterases and general proteins (Nyman 1967; Nyman 1970; Payne et al. 1972; Nygren et al. 1975). Subsequent papers also reported distinct patterns for glucosephosphate isomerase (Guyomard 1978; Beland et al. 1981; Taggart et al. 1981) and phosphoglucomutase (Guyomard 1978). The tissue samples were taken from muscle, liver, or blood after killing the fish. Blood can also be drawn from a live fish but this is still troublesome. Further, a method of nonlethal muscle biopsy has been described (Crawford et al. 1977). These methods operate well, however, only with adult fish.

The purpose of our study was to increase the capability for electrophoretic identification of salmon and brown trout and

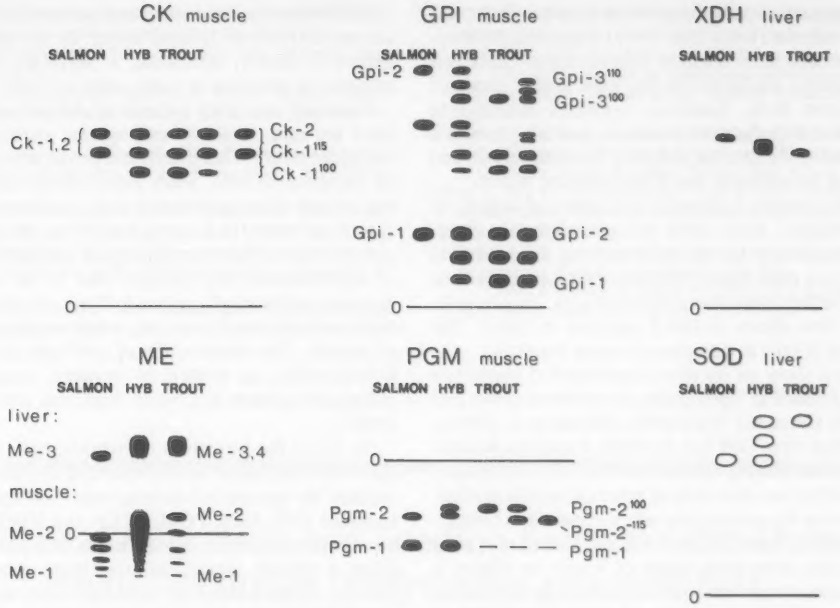

FIG. 1. Observed electrophoretic phenotypes in Atlantic salmon (*Salmo salar*), brown trout (*S. trutta*), and their hybrids for enzymes, which show different electrophoretic migration. The anode is above the origin in all cases. A lithium hydroxide–boric acid buffer was used for CK, GPI, and XDH and an amine–citrate buffer for ME, PGM, and SOD.

their hybrids. Our aim was to describe new diagnostic enzyme systems and a nondestructive easy sampling method that can be used with juvenile fish as well as adults.

Materials and Methods

Brown trout were from three different stocks. Thirty-one wild and 181 hatchery-reared fish from a lake-dwelling Pielisjoki stock were studied (for further details see Vuorinen 1984). Two anadromous brown trout samples (30 of each) were obtained from Ohtaoja hatchery. They represent stocks native to the Tornionjoki and Iijoki rivers, both of which drain into the northern Baltic Sea. Mature landlocked salmon (65) were caught from the Pielisjoki river, Eastern Finland, from 1980 to 1983 (see also Vuorinen 1982). Additionally, three hatchery samples (60 fish of each) of this stock were also analyzed. Two of them were offspring of Laukaa and Ohtaoja hatchery broodstocks whereas fishes from Kontiolahti hatchery were progenies of wild salmon. Anadromous salmon native to the Tornionjoki River were obtained from Ohtaoja hatchery. From this stock we studied 10 broodstock fishes and 30 of their progeny. Electrophoresis revealed inadvertently produced salmon × trout hybrids among the Tornionjoki broodstock and landlocked salmon from the Laukaa hatchery.

In addition to the usual muscle and liver samples some adipose fin biopsies from adult fishes were taken. Only the outermost 3–5 mm of the adipose was used; this can be taken without damaging the fish. The samples were stored at −40°C until analyzed. The electrophoretic conditions, tissue specificity of enzymes, and appropriate buffer systems were described in detail by Vuorinen (1982, 1984). The buffers used in our study included (A) a discontinuous lithium hydroxide – boric acid buffer, pH 8.1, (B) an amine–citrate buffer, pH 6.1, and (C) a Tris–citric acid buffer, pH 7.1.

A total of 14 enzyme systems were stained: alcohol dehydrogenase (ADH), aspartate aminotransferase (AAT), creative kinase (CK), glycerol-3-phosphate dehydrogenase (G3P), isocitrate dehydrogenase (IDH), lactate dehydrogenase (LDH), malate dehydrogenase (MDH), malic enzyme (ME), phosphoglucomutase (PGM). phosphogluconate dehydrogenase (PGD), glucosephosphate isomerase (GPI), sorbitol dehydrogenase (SDH), superoxide dismutase (SOD), and xanthine dehydrogenase (XDH). Enzyme assays followed the recipes of Allendorf et al. (1977).

Results and Discussion

The locus identification follows that of Vuorinen (1982, 1984). If the nomenclature is not the same for both species, that of brown trout is used and the corresponding locus for salmon is given in parentheses. The following loci were identically monomorphic for both species: *Adh*, *Ck-1*, *G3p-1*, *G3p-3* (*G3p-3,4*), *Idh-1,2* (*Idh-1*), *Idh-3,4* (*Idh-2,3*), *Ldh-1*, *Ldh-3,4*, *Mdh-1*, and *Pgd*. Also identical were the common forms of *Aat-4* (*Aat-3*), *G3p-2*, *Ldh-2*, *Mdh-2*, *Mdh-3,4*, and *Sdh-1,2*, of which all except SDH were polymorphic in brown trout. In salmon, AAT and SDH were polymorphic, and according to Ståhl (1983) these variant alleles are common in many other populations in northern Europe. Assays for CK, GPI, ME, PGM, SOD, and XDH showed distinct zymograms for salmon and trout (Fig. 1). The adipose fin biopsies revealed activity for the following loci, which are most strongly expressed in liver: *Gpi-3* (*Gpi-2* in salmon), *G3p-3*, *Ldh-3,4*, *Mdh-3,4*, and *Pgd*. Among these, GPI is diagnostic between salmon and trout.

Muscle CK appears as a duplicate locus in brown trout and probably also in salmon (Utter et al. 1979). Common homozygotes are three-banded in brown trout whereas salmon have two bands with mobilities similar to the two most anodal bands of brown trout. Trout have, however, a variant homozygote (*115/115*) identical with the salmon pattern, and this prevents a reliable separation of the species. A hybrid between salmon and the common trout homozygote has a three-banded pattern.

GPI, a dimeric enzyme, possesses two zones of activity in salmonids. In muscle, both zones are present but in liver, activity is expressed only for the faster moving zone. Muscle extracts from brown trout usually produce a six-banded pattern that presumably reflects the presence of three loci. Taggart et al. (1981) reported five alleles at *Gpi-2* and two at *Gpi-3*. The variant allele *Gpi-3(110)* is also present in our material.

Atlantic salmon show an invariant three-banded phenotype that is usually explained as representing the products of two loci (Guyomard 1978; Cross and Ward 1980). Beland et al. (1981), however, identified three GPI loci in North American Atlantic salmon. It is possible that the least anodal GPI zone of Atlantic salmon is encoded by two loci as in all other salmonids studied. This assumption can be verfied only when variation is found.

The species differ at both GPI zones: in the least anodal zone brown trout usually show three bands of which the fastest is identical to the salmon band. In the most anodal zone the salmon isozyme is faster than the products of trout *Gpi-3(100)* or *Gpi-3(110)*. The F1 hybrid between salmon and the common homozygote trout reveals a summation of parental patterns with 10 bands. Staining for GPI provides, therefore, an effective way to identify salmon, trout, and their hybrids. The diagnosis is also possible from live fish by using adipose fin biopsies, which show good activity for the most anodal GPI locus.

For the malic enzyme, two zones of activity are observed. The least anodal zone is of mitochondrial origin (Cross et al. 1979). It is encoded by two loci producing a pattern of five isozymes with decreasing cathodal activity. The homotetrameric product of *Me-2* in trout is faster than that of salmon whereas the products of *Me-1* have identical mobilities. The zymogram of a hybrid fish is blurry due to the 30 bands expected. For salmon, a variant allele *Me-2(115)* has been identified by Cross et al. (1979) but it was absent in our material.

When using B buffer both anodal and cathodal zones of PGM activity are produced. However, the interpretation of the liver specific anodal zone is prevented by low enzyme activity. In the cathodal zone, salmon tissues show two bands. They are designated as products of *Pgm-1* and *Pgm-2* (Allendorf et al. 1982). *Pgm-2* corresponds to the traditional salmonid PGM locus, where a variant allele has been reported for Atlantic salmon (Ståhl 1981). Brown trout reveals only one strong band, which is slightly less cathodal than salmon *Pgm-2*. Trout *Pgm-1* is represented only by a very weak band. At trout *Pgm-2* a variant allele *(−115)* was found whose product is faster than that of salmon *Pgm-2*. The hybrids show both parental bands but due to slight mobility differences, side-by-side comparisons are recommended to distinguish possible hybrids.

Salmonid livers show two zones of activity for SOD. We consider here the faster and more active isozyme. The zone is identical in both species when using traditional A buffer. In B and C buffers, however, the brown trout isozyme moves faster and the hybrids express a three-band pattern typical for a dimeric enzyme. Among Swedish brown trout an allele *50* has been reported (Allendorf et al. 1977) but its mobility compared with salmon SOD remains to be clarified.

XDH shows a fixed one-band pattern for both species. The salmon enzyme is located closer to the anode. The hybrid pattern is blurry, indicating a polymeric structure for the enzyme, as observed in many other animals.

Naturally occurring hybrids of Atlantic salmon and brown trout are rare, even if both species spawn jointly in many European rivers. This manifest reproductive isolation may now be disturbed by man, since many salmon and trout stocks are maintained or supplemented with hatchery fish. When both species are reared in the same hatcheries, mixing them is always possible due to their morphological similarity. The probability of hybridization may increase also in the wild as spawning grounds are drastically reduced. The remaining places may then be shared between the species, which would ease the formation of hybrids. The introduction of new species can also result in hybridization, as evidenced between introduced trout and indigenous salmon in a North American river by Beland et al. (1981).

To detect the formation of hybrids, both in the wild and in hatchery conditions, an accurate and fast method is needed to separate the species and their hybrids. Our study shows that five enzymes (ME, GPI, PGM, SOD, and XDH) have diagnostic electrophoretic patterns for Atlantic salmon and brown trout that allow a reliable identification of these species and their F1 hybrids. From these, only GPI and PGM have formerly been reported as species specific. At four of these five enzymes some variation has been described, but this does not prevent an accurate identification. The most anodal locus of GPI exhibited good activity also in adipose fin biopsies, which can be sampled without killing or maiming the fish. The diagnosis, therefore, is also possible from live fish, both juvenile and adult. Recently, the identification of salmon and trout eggs through their GPI zymograms has been reported by Mork and Heggberget (1984).

NOTE ADDED IN PRESS: See also the following recent paper: W. W. Crozier. 1984. Electrophoretic identification and comparative examination of naturally occurring F hybrids between brown trout (*Salmo trutta* L.) and Atlantic salmon (*S. salar* L.). Comp. Biochem. Physiol. 78B: 785–790.

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Diel Vertical Migration and Feeding Behavior of a Demersal Hydromedusan (*Polyorchis penicillatus*)

S. A. Arkett

Department of Zoology, University of Alberta, Edmonton, Alta. T6G 2E9[1]
and
Bamfield Marine Station, Bamfield, B.C. V0R 1B0

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The hydromedusan *Polyorchis penicillatus* makes a small amplitude diel vertical migration. During the day, over 85% of the individuals were observed within 1 m of the bottom, while at night, medusae diffused several metres up into the water column. This movement occurred concomitantly with the emergence of many of the major taxa of demersal zooplankton whose activity was quantified by emergence traps. Food boli contents collected from *Polyorchis* showed some selectivity for large, fast-moving demersal plankters and low capture and utilization of invertebrate larvae. Diel shifts in feeding behavior and water column position enable *Polyorchis* to feed efficiently on high densities of demersal plankters at all times. Medusae may be exempt from migration constraints imposed by visual predators and are thus able to move into areas of high prey density to supply energetic requirements. Hydromedusae, such as *Polyorchis*, are shown to utilize a variety of factors, such as tentacle position and swimming speed, in an "ambush" strategy to optimize prey encounters.

L'hydroméduse *Polyorchis penicillatus* effectue une migration verticale de faible amplitude au cours du cycle nycthéméral. Le jour, plus de 85 % des hydroméduses se trouvent dans une couche de 1 m au fond de l'eau, tandis que la nuit, elles se dispersent dans une couche de plusieurs mètres. Ce mouvement se produit simultanément avec l'apparition d'un grand nombre d'animaux appartenant aux principales espèces zooplantoniques de fond dont l'abondance a été quantifiée au moyen de pièges conçus pour les capturer à leur émergence. L'étude du contenu stomacal de *Polyorchis* a montré qu'elles se nourrissent plutôt d'organismes planctoniques de grande taille qui vivent sur les fonds et se déplacent rapidement, et qu'elles capturent peu de larves d'invertébrés. Grâce à la variation nycthémérale de leur alimentation et de leur position, les hydroméduses (*Polyorchis*) peuvent en tout temps trouver amplement d'organismes planctoniques de fond pour se nourrir. Les méduses n'ont ainsi pas besoin de se déplacer comme le doivent les prédateurs qui chassent à vue, de sorte qu'elles peuvent migrer vers les zones où leurs proies sont abondantes pour trouver la nourriture nécessaire à leurs besoins énergétiques. On montre aussi comment elles tirent partie de divers facteurs tel que la position de leurs tentacules et leur vitesse de nage pour optimiser les rencontes avec leursproies, chassant par « ambuscades.»

Received April 11, 1984
Accepted August 17, 1984
(J7753)

Reçu le 11 avril 1984
Accepté le 17 août 1984

[1]Present address.

Gelatinous zooplankters have often been overlooked in descriptions of diel vertical migrations even though they are frequently abundant members of the plankton. This may be due in part to their frailty and destruction when collected in plankton nets. There are, however, a few detailed accounts of vertical migrations of medusae. Russell (1925), Moreira (1973), and Mills (1982), all using plankton tows, reported distinct diel vertical migrations of numerous species of hydromedusae. Yasuda (1973) found that a scyphomedusa, *Aurelia aurita*, rises during the day and sinks at night, a reversed diel migration. These studies used plankton nets often taking samples tens of metres apart, which may underestimate the numbers and distort the population distribution. Medusae that migrate only short distances or are close to the bottom may be considered nonmigratory or are missed altogether with this sampling method. Hamner et al. (1975) and Mackie and Mills (1983) have circumvented these problems and have shown the usefulness of direct field observations for studying migrations, aggregations, and behavior of medusae and other gelatinous zooplankton. Studies using large containers (Mackie et al. 1981; Mills 1983) have also been useful in observing diel migration of medusae. Although it is clear that some medusae do migrate throughout the water column in a coordinated manner, the adaptive value of these migrations has not been demonstrated.

One possible advantage to diel migration and concurrent changes in feeding behavior may be to increase prey encounters. Medusae exhibit a wide variety of feeding behavior (Fraser 1969; Mackie 1980; Mills 1981; Bailey and Batty 1983), but most medusae feed using some form of "sink-fishing," a behavior in which the tentacles are extended and catch prey on contact as the individual sinks through the water column. The number of prey encountered and the types of prey captured by medusae then depend on tentacle number, tentacle orientation, behavior during sink-fishing bouts, and water column position. Because most medusae are purely planktonic, they feed, using some form of sink-fishing, almost exclusively on small plankters. Yet, some medusae have specialized to use other resources. One such medusa is *Haliclystus*, which has adopted a semisessile mode and relies on drifting plankton. The small trachymedusan *Tesserogastria* rarely swims; instead it occupies mud surfaces and eats small infauna (Hesthagen 1971). Hydromedusae of the genus *Polyorchis* also spend much of their time at or near the bottom, but unlike other bottom-dwelling medusae, they are also active swimmers. The food boli contents of *Polyorchis karafutoensis*, found in the western Pacific, are indicative of this bottom-dwelling behavior. Large, demersal plankters as well as purely planktonic forms are regularly found within its manubrium (Zelickman 1976). The hydromedusan *Polyorchis penicillatus*, commonly found near the bottom of shallow, muddy bays on the west coast of North America, also often has large demersal crustaceans in its manubrium. Mills (1983), using large cylinders, observed diel movements of *Polyorchis* and suggested that capture of and feeding on demersal plankters by *Polyorchis* may be facilitated by its movements in the water column. The diel migration of *Polyorchis* and its unusual bottom-affinity behavior may be a unique adaptation to utilize a resource not commonly exploited by other medusae. The purpose of this study was to determine the extent of the diel vertical migration of *Polyorchis* in the field and to correlate its movements with those of its principal prey.

I directly observed a small amplitude diel vertical migration of the hydromedusan *P. penicillatus*. The migration occurs concomitantly with that of demersal plankters, which are the principal prey of *Polyorchis* as determined from the contents of food boli. I relate some of its feeding behavior observed in the field to the feeding strategy used by ambush predators.

Materials and Methods

The study area in Bamfield Inlet, Bamfield, B.C. (48°49′N, 125°08′W) has a soft mud bottom with *Zostera marina* along the edges. Occasional macroalgal "islands" of *Agarum cribrosum*, *A. fimbriatum*, *Macrocystis integrefolia*, and *Laminaria saccharina* are found on an otherwise nearly homogeneous bottom. Depth of the sampling area ranged from 6 to 10 m, depending on the tide.

The vertical distribution of *Polyorchis* was determined visually using SCUBA. Vertical columns of water were defined by a weighted float-line marked at 1-m intervals and the bottom 1 m into 0.5-m intervals. Ten to 20 replicate columns were made at the study site at nine day (08:30–20:30) and nine night (20:30–08:30) periods during late July and August 1982. The position of each replicate column in the study area was randomly selected by a surface diver. For each replicate column a second diver moved vertically down and up the float line counting the number of individuals observed within 1 m^3. This area was defined by the float line and a PVC frame. A dive-light was mounted on the frame during the night and during periods of low visibility.

Behavioral observations of *Polyorchis* were made by divers during the day. Divers maintained neutral buoyancy and observed undisturbed single individuals for 10 min. The total number of swimming contractions during this time was recorded. A total of 39 individuals over 10 dives were observed at various times of the day.

Emergence traps, modeled after those designed by Alldredge and King (1980), were used to determine the composition and abundance of demersal zooplankton. Emergence traps, without the catch-bottles, were slowly lowered to the bottom site by divers. Replicate traps were placed less than 2 m from each other. Once a trap was on the bottom, the base was forced into the mud to ensure a seal from surrounding water. Catch-bottles filled with filtered (110-μm Nitex mesh) seawater were sealed and transported to the traps. Seals were broken and catch-bottles put into place. The catch-bottle opening was 0.5 m from the substratum. This procedure was followed throughout sampling to prevent disruption of the flocculent, bottom mud. At the end of a sampling period, the catch-bottles were removed from traps, immediately sealed, and transported to the surface. Bottle contents were filtered through 110-μm Nitex mesh and fixed in 10% formalin with rose bengal. The traps were repositioned, catch-bottles refilled, and replaced onto traps. Samples were sorted to major taxonomic groups, counted, and the total number of individuals per square metre was determined. A single sampling run consisted of two consecutive days yielding two night (20:00–08:00) and two day (08:00–20:00) samples with three trap replicates for each sample. Three such runs were made during late July and August 1982.

Ten to 20 individual *Polyorchis* having a visible food bolus were collected concurrently with each day and night sample. The food boli were removed from individuals and fixed in 10% formalin with rose bengal. Boli contents were later examined, and nearly whole, identifiable individuals were counted.

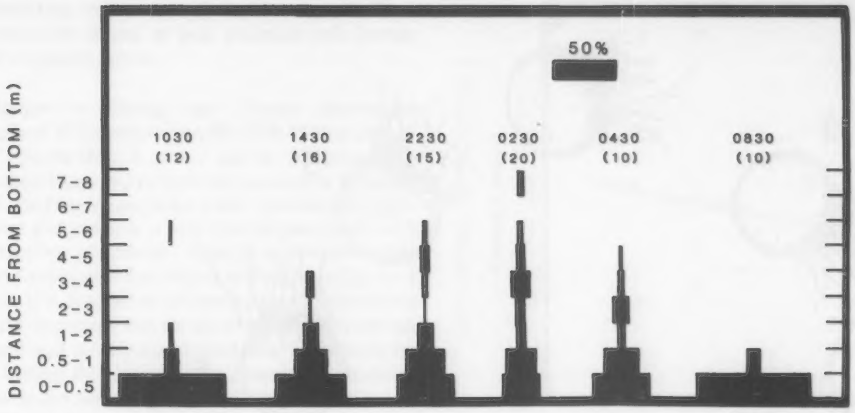

FIG. 1. Mean percentage of individual *Polyorchis* sighted at each depth during selected sampling periods from 21 July to 27 August 1982 in Bamfield Inlet. Time of each sampling period is shown above the columns, and the number of replicate columns for each sampling period is shown in parentheses. Sunset was approximately 19:00 and sunrise 06:00.

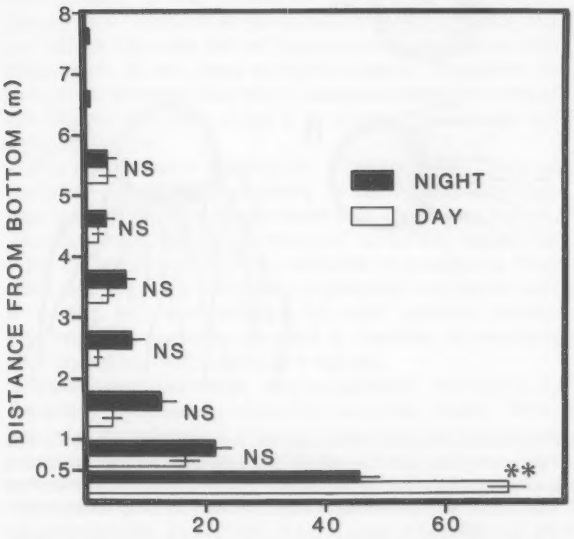

FIG. 2. Mean percentage (±1 SE) of individual *Polyorchis* sighted in the water column during nine day (08:00–20:00) and nine night (20:00–08:00) samples from 21 July to 27 August 1982 in Bamfield Inlet. Day–night comparisons between mean percentage of individuals at each depth were made using the Wilcoxon two-sample test (Sokal and Rohlf 1969) (**$p < 0.01$, NS = $p > 0.05$). Pooled number of column replicates for day and night were 100 and 111, respectively. The average depth of the water column during day and night samples was nearly identical at 8.3 and 8.2 m, respectively.

TABLE 1. Mean number (± SE) of individuals/m^2 of bottom collected in demersal plankton emergence traps during day (08:00–20:00) and night (20:00–08:00) in Bamfield Inlet. Numbers have been pooled over three separate 2-d sampling periods from late July and August 1982 with a total of 18 replicates for day and night samples. The total number of identifiable prey items within food boli from *Polyorchis* collected at 08:00 for night and 20:00 for day samples are shown in parentheses. p indicates a presence, but total numbers not determined. **$p < 0.01$; NS = $p > 0.05$.

Taxon[a]	Night	Day	
Calanoid copepods	3540±645 (p)	2567±573 (p)	NS
Cyclopoid copepods	282±54 (p)	120±16 (p)	**
Harpacticoid copepods	521±71 (p)	278±19 (p)	**
Gammarid amphipods	106±18 (5)	6±1 (10)	**
Cumaceans	9±2 (33)	0.4±0.5 (15)	**
Ostracods	22±3 (25)	1±0.5 (4)	**
Zoea larvae	132±43 (36)	54±9 (20)	NS
Cyprids	15±3 (199)	9±2 (94)	NS
Polychaete sp. 1	7±2 (3)	1±0.5 (4)	**
Polychaete sp. 2	14±4 (2)	0.4±0.2 (1)	**
Nauplii	925±173 (36)	1316±174 (21)	**
Rotifers	332±94 (0)	817±192 (0)	NS
Polychaete sp. 3	13±2 (1)	43±5 (0)	**
Spionid larvae	6081±987 (210)	12684±2687 (0)	NS
Veligers	1189±256 (30)	1968±141 (0)	**
Tanaids	0 (6)	0 (2)	
Caprellid amphipods	0 (10)	0 (4)	

[a]Polychaete sp. 1 is *Ophiodromus pugettensis*, sp. 2 is from Opheliidae, and sp. 3 is from Sphaerodoridae.

Results

Migration patterns of Polyorchis — Densities of 2–5 individuals/m^3 were regularly observed; however, large aggregations of up to 64/m^3 were not uncommon. These large aggregations were most often found close to the bottom and clustered around *Agarum*. Most individuals counted were larger than 1.0 cm bell height. Consistent visual observations of smaller individuals proved too difficult.

The diel movements of *Polyorchis* were of low amplitude and generally confined to the area within several metres of the bottom (Fig. 1). There was an upward movement several hours after dusk that resulted in a more diffuse and even distribution in the water column throughout the night. Just after dawn, individuals were found very close to the bottom and usually remained in this position throughout the day. Pooled night and daytime samples (Fig. 2) show increases in the percentage of

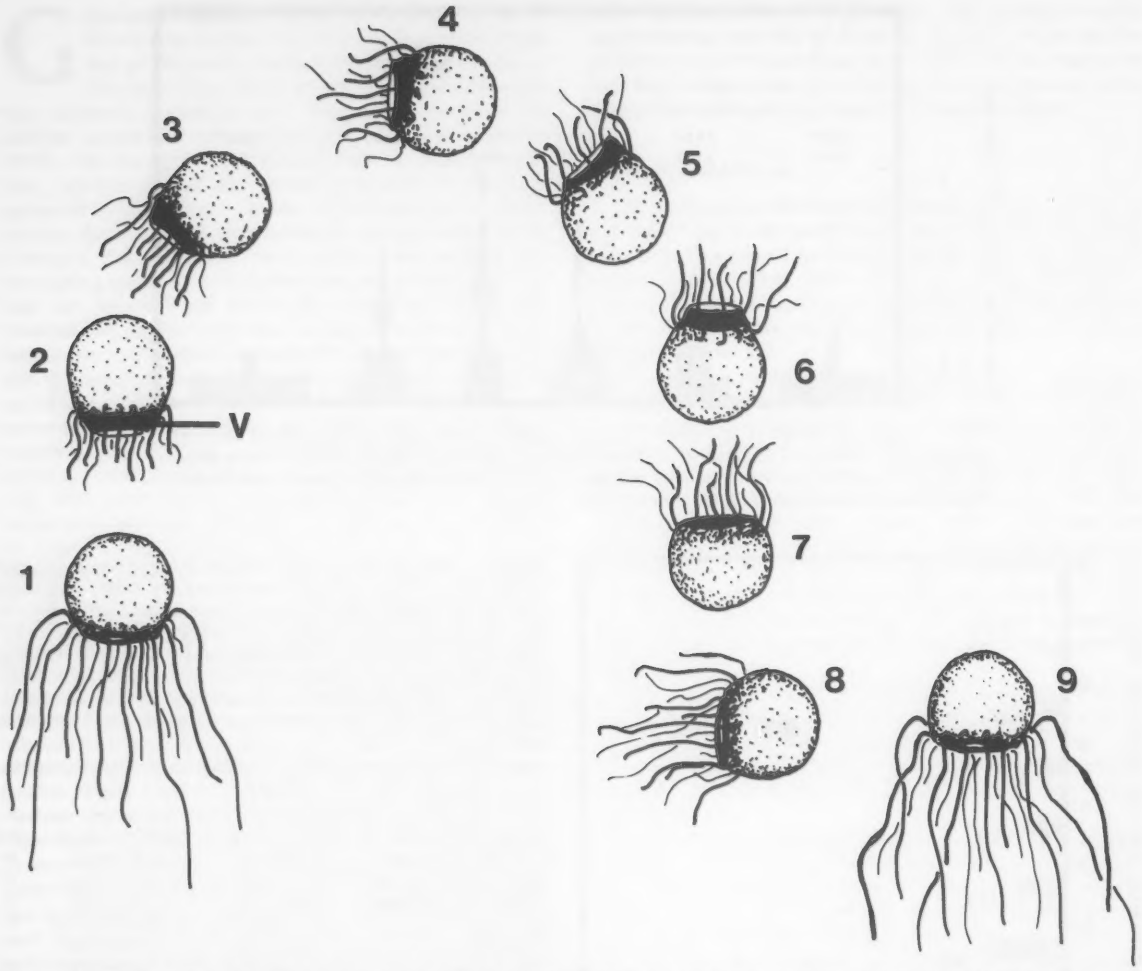

FIG. 3. Schematic pathway of an extended swimming bout exhibited by *Polyorchis* during observation periods. An individual is shown at rest (1) before the bout with its tentacles extended in the sink-fishing posture. A swimming bout spontaneously begins with tentacles fully contracted (2). Asymmetrical velar contractions (3–5) cause the individual to swim in an arc until it is swimming directly downward (6). This downward swimming spontaneously stops (7), and tentacles begin to relax as the bell returns to its original orientation (8). Tentacles are fully relaxed while the fishing posture and low frequency maintenance swimming is resumed (9). V = velum.

individuals in the water column at night, while during the day, over 85% of the individuals were within 1 m of the bottom.

Demersal plankton emergence — The major taxa of demersal plankters consistently showed two distinct emergence activity patterns (Table 1). Those that emerged at night constituted the larger group, with copepods caught in the greatest numbers. Most of the large, fast-moving demersal taxa (e.g. gammarid amphipods, cumaceans, ostrocods, two species of polychaetes) showed significant nighttime increases in abundance (Table 1). Larval or juvenile stages of invertebrates were consistently captured in greater numbers during the daytime. Spionid larvae and veligers were often very abundant. Other organisms occasionally captured included cladocerans, larvaceans, and megalops.

Food bolus contents — Bolus contents consisted primarily of crustacean exoskeleton fragments tightly bound with mucus. Contents were in various stages of digestion, with the greatest degree of digestion found in the proximal portion of the manubrium (nearest gonad attachment). Most of the intact contents were found in the distal portion of the manubrium; however, some items such as spionid larvae, veligers, ostracods, and cyprids were found intact at the proximal end as well.

Organisms within food boli were similar to those found in demersal trap samples, regardless of the time collected (Table 1). Nighttime increases in numbers of cumaceans, ostracods, zoea larvae, and cyprids collected in traps, however, corresponded with increases in numbers of individuals present within food boli. Copepod fragments were present in all food boli, but no attempt was made to quantify day–night differences. Daytime food boli were almost totally devoid of groups with increased daytime activity, whereas the presence of larvae within food boli increased at night. Caprellid amphipods and tanaids were consistently found within boli both during the day

and night, but these taxa were never collected in the traps. Other organisms occasionally found in boli included fish larvae, nematodes, and megalops larvae.

Feeding behavior — During each 10-min observation period, individuals of *Polyorchis* spent 90–95% of their time in a "sink-fishing" posture (Fig. 3, nos. 1 and 9). Tentacles were held outward at their bases and more distal portions of tentacles drop downward. Drifting through the water, individuals maintained this posture and swam at a very low frequency of 3–15 swimming contractions per minute. Smaller individuals swam at slightly higher frequencies than larger individuals (Fig. 4). I will refer to this low frequency swimming as "maintenance swimming," as the frequency was far too low to result in any net upward movement and merely maintained their position in the water column. During this maintenance swimming, medusae usually remained at the same depth or sank very slowly.

The sink-fishing posture was disrupted by occasional contact with bottom obstructions (e.g. "islands" of *Agarum*, logs, sea anemones) and usually resulted in one to two very rapid swimming contractions. These swimming contractions resulted in upward movements of several centimetres. Tentacles were often partially or fully contracted during these brief swims. Local currents sometimes moved and entangled tentacles over the bell, or tilted the bell off vertical orientation. These disorientations did not cause extensive tentacle contractions or changes in swimming frequency. Animals continued to swim at low frequencies while, owing to its center of gravity, the bell righted passively.

Prey also disrupted the tentacles. When small prey contacted tentacles, only tentacles involved in handling the prey contracted while the remaining tentacles held their fishing posture. The manubrium then made "searches" of the bell margin and made the transfer of prey from tentacles to manubrium. Only when large prey such as caprellid or gammarid amphipods came in contact with the tentacles did more tentacles become involved. This sometimes resulted in cessation of swimming and "crumpling" with subsequent sinking.

Maintenance swimming was occasionally interrupted by apparently spontaneous extended swimming bouts. Thirty percent of the individuals observed showed one to four separate extended swimming bouts during the 10-min periods. These extended swimming bouts consisted of 10–20 swimming contractions at a frequency much higher than that of maintenance swimming. Individuals swam at a rate of between one and two swimming contractions per second depending on the size of the individual, with smaller medusae again swimming at greater frequencies than larger individuals. In these extended swimming bouts (Fig. 3), the first few contractions were usually symmetrical and only moved the individual several centimetres. After several contractions, obvious asymmetrical velar contractions caused individuals to turn in an arc with a diameter of about 20–30 cm, finally resulting in downward swimming. At this point, contractions ceased spontaneously, the bell righted to the original orientation, tentacles relaxed, and maintenance swimming resumed in the sink-fishing posture. This extended swimming bout did not usually result in a net vertical displacement, but it did move the medusa laterally. Variations on this general pattern were also observed. Some individuals did not make the downward turn, but continued to swim vertically. A continuation of downward swimming was also observed, often to the point where they were swimming against the substratum. Individuals also sat on their tentacles directly on substrata while

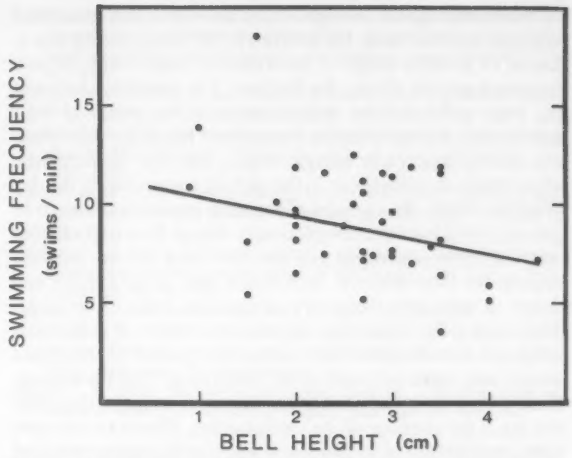

FIG. 4. Swimming frequencies of 39 various sized individuals of *Polyorchis* during "maintenance swimming." Frequency was averaged over 10-min field observation periods. $Y = 11.48 - 0.97X$, $r = 0.323$. Regression is significant at $p < 0.05$.

the manubrium made searches around the bell margin and across the substratum.

Discussion

It is clear that *P. penicillatus* undergoes a small amplitude diel vertical migration within several metres of the bottom with an upward movement beginning after dusk and lasting throughout the night. Just after dawn, *Polyorchis* is down near the bottom where it remains throughout the day. This type of migration would have been missed by conventional sampling methods. Diel vertical migration of medusae has been documented most often by remote collection gear such as plankton nets, and for robust species migrating large distances, this method of sampling may be adequate. However, species with small amplitude migrations, such as *Polyorchis*, may be missed or considered nonmigratory due to the poor depth resolution of plankton tows. Demersal species may also be missed or damaged due to net-fouling by sediment or obstructions on the bottom. Direct observations of plankton through the use of SCUBA (Hamner et al. 1975; Omori and Hamner 1982) and submersibles (Mackie and Mills 1983) have eliminated some of these problems. Yet, some problems with direct observation of zooplankton distributions remain. A large number of sample replicates are often required to establish the distributional patterns amongst low density individuals, but replication is costly and time consuming and these considerations precluded the detection of the precise timing of vertical movements in my study. The improved temporal resolution of movements in Mills' (1983) tank study, however, showed that *Polyorchis* moves upward just after dusk and downward just after dawn.

Data from emergence trapping show the typical diel activity pattern of most plankters with increased nighttime activity of several groups of large, mobile demersal plankters. Their marked absence or reduced numbers during daylight hours indicate that these groups either remain in or on the sediments or make only very short forays in the water column. The timing of upward and downward movements was not determined, but Alldredge and King (1980) found that most polychaetes and gammarid amphipods emerged just after dusk and returned to

sediments throughout the night. They also found that cumaceans emerged just after dusk, but returned to the bottom during dawn. Larval or juvenile stages of invertebrates consistently showed increased activity during the daytime. The sampling design of the traps precluded the determination of the extent of their movements, but most marine invertebrate larvae are photopositive during their early pelagic stages, and this characteristic allows them to concentrate in the surface waters during the day (Thorson 1964). Two groups of demersal plankters known to be present in the Inlet but conspicuously absent from trap samples were caprellid amphipods and tanaids. There are two possible reasons for their absence. Individuals may avoid capture and return to sediments when they contact the walls of the traps. This "wall effect" may then depress the number of individuals collected. Another possibility is that individuals from these two groups may make only very short forays away from the bottom. Even if they do in fact become more active at night, they may not reach the opening of the catch-bottles. However, for most large, mobile taxa (e.g. gammarid amphipods, cumaceans, and polychaetes), it is clear that daytime movements are restricted to less than 0.5 m from the bottom, while nighttime movement is at least this far and probably farther.

The primary adaptive advantage of the diel vertical migration of *Polyorchis* is probably the optimization of prey encounters by matching movements with its principal prey, demersal plankton. The positional shift, albeit of small amplitude, is sufficient to allow two different feeding modes and may permit prey selectivity. Clearly, the planktonic sink-fishing behavior enables *Polyorchis* to capture items swimming in the water column. Sink-fishing is probably most advantageous during the night when most of the demersal plankton is moving, but this behavior yields to a greater dependence on substratum feeding during the day. The bottom-sitting behavior of *Polyorchis* has been observed before and is referred to as "landing" (Zelickman 1976) or "perching" (Mills 1981). Perching may be seen at anytime, but it is most important during the day when many of the prey are very close to the bottom or clinging to various substrata. Feeding close to or directly from substrata explains the presence within food boli of prey items (e.g. caprellid amphipods, tanaids) that are either nonmigratory or live close to or on substrata. This feeding mode may, however, not normally be as efficient as sink-fishing, except when *Polyorchis* lands on *Agarum* "islands" or other debris. The mechanism for the shifts from planktonic sink-fishing to perching or extended swimming bouts remains enigmatic. Many medusae go through cycles of some form of sink-fishing interspersed with active swimming (Zelickman 1976; Mackie 1980; Mills 1981). A possible explanation of these shifts is that individuals can detect prey densities by the frequency of encounters. If they enter areas of low encounters, they may make a "decision" to move, and this is seen as an extended swimming bout. The large aggregations of medusae observed near *Agarum* "islands" also suggest that *Polyorchis* will remain in areas where prey density is high.

Study of the contents of food boli indicates that there may be some differential selection and utilization of prey items. Gammarid amphipods and cumaceans may be selectively captured, as in some cases greater numbers of individuals were found in food boli than in trap samples. Larval or juvenile stages appear to be of minor importance as prey because few were found in food boli relative to the number collected in traps. Larval defences such as veliger shells or setae of spionid larvae may deter capture if nematocysts cannot penetrate shells or extend past setae. Larvae may also escape predation by moving into surface waters during the daytime, thereby avoiding high concentrations of *Polyorchis* near the bottom. Most medusae may also not be able to effectively sink-fish in surface waters because turbulence may disrupt tentacle position and cause "crumpling" and sinking. Even though larval stages are occasionally captured, they may not be useable to *Polyorchis*. Many of the spionid larvae, veligers, and cyprids, though occasionally taken in large numbers, were found intact even at the proximal end of the bolus.

"Energetic" models have been invoked to explain the adaptive value of migrations, but they have been largely restricted to grazing plankters (Enright 1977). Medusae clearly are not under the same constraints as grazers, but may migrate to meet their energetic requirements. These energetic models have rivaled the "predator avoidance theory" (Zaret and Suffern 1976). Highly mobile and visible plankters, such as many demersal species, avoid predation through seclusive behavior during the daytime. These individuals then emerge to feed, spawn, or disperse during the night when the probability of detection is less. *Polyorchis* is probably visible and vulnerable to predation at any of its daytime positions in the water column. Nematocyst-laden tentacles may, however, deter predators, such as fish, and allow diel movements with impunity.

In addition to optimizing prey encounters, the diel migration of *Polyorchis* may also afford some advantage by synchronizing spawning locations. Mills (1983) found that *P. penicillatus* spawns in the hour immediately after dark and that spawning is complete within 10 min. Concurrent movements of individuals together with very strong species specificity of sperm attraction (Miller 1980) may ensure a high percentage of insemination. Nighttime movement away from the flocculent substratum may also be important in preventing gamete loss.

The unusual demersal feeding behavior of *Polyorchis* described in this study illustrates one example of the wide variety of behaviors used by predacious zooplankton to concentrate and capture prey. The planktonic sink-fishing posture of *Polyorchis* may serve as a model in the explanation of how most planktonic medusae optimize prey capture. Gerritsen and Strickler (1977) and Gerritsen (1980) have suggested several factors that affect the probability of contacting prey: swimming speed and direction, encounter radius, and prey density. All but prey density are behavioral factors and are controlled by the individual predator. Medusae utilize various combinations of these factors to increase their prey encounters (Fraser 1969; Mills 1981; Bailey and Batty 1983). The demersal feeding behavior of *Polyorchis* illustrates how these factors may be used by medusae for specialized feeding on demersal plankton. Gerritsen and Strickler's (1977) model predicts two energetically optimal swimming strategies for invertebrate zooplankton predators: "ambush" and "cruising." *Polyorchis* and most medusae are typical ambush predators: those that move slowly relative to their prey items. *Polyorchis* remains nearly motionless in the water column except for the low frequency maintenance swimming and slow sinking. This movement is very slow relative to principal prey items, the large, fast-moving demersal plankters (e.g. cumaceans, gammarid amphipods). Gerritsen (1980) also predicted that the highest encounter rate results when predator and prey items swim perpendicular to each other. For a sink-fishing medusa like *Polyorchis*, the sinking is slow enough that there may be little advantage gained from this; however, the tentacle arrangement while sink-fishing may increase encounter rates by its orthogonality to prey movements.

Tentacle arrangement during sink-fishing may increase encounter rates by altering the encounter radius. Encounter radius, as defined by Gerritsen and Strickler (1977), is a composite of various sensory systems, habitat conditions, and prey type, but for sink-fishing predators like *Polyorchis*, it may be simplified to the area of tentacle extension (Fig. 3). The cylindrical arrangement of tentacles consists of both horizontal and vertical components. These components provide orthogonal placement of tentacles and capture prey items moving vertically and horizontally. A large individual with a bell height of 4.0 cm in a typical sink-fishing posture can fully extend its tentacles 12–15 cm downward and held outward in a 9- to 11-cm-diameter circle. This posture can effectively capture all prey items in a cylindrical area of 750–1500 cm^3. If individuals become aggregated in large numbers, they may fish out large volumes of water. These large aggregations may be influential in reducing larval fish stocks and other plankters (Plotnikova 1961; Sveshnikov 1963; Zelickman 1969; Bailey and Batty 1983).

Acknowledgments

I thank J. Elliot for his invaluable assistance in diving and counting plankton, W. C. Mackay and A. R. Palmer for discussions and manuscript criticism, and R. A. Foreman for providing facilities at Bamfield Marine Station. This study was supported by National Sciences and Engineering Research Council of Canada grant A-0419 to A. N. Spencer.

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Mortality Estimation: Biased Results from Unbiased Ages

Jay Barlow

U.S. National Marine Fisheries Service, Southwest Fisheries Center, P.O. Box 271, La Jolla, CA 92038, USA

Barlow, J. 1984. Mortality estimation: biased results from unbiased ages. Can. J. Fish. Aquat. Sci. 41: 1843–1847.

Estimates of mortality rates from age distributions are biased by imprecision in age estimation, even if age estimates are unbiased. I have derived a method for predicting the magnitude of this bias from information on the precision of age determination. Monte Carlo simulations show that bias can be accurately predicted. The commonly used Chapman–Robson mortality estimator is shown to be robust to imprecision in age determination if all age-classes are included. Errors are likely, however, if one or more age-classes are excluded or if other mortality estimators are used. Biases can be corrected if the distribution of age-estimation errors is known.

L'estimation des taux de mortalité d'après les distributions des âges est biaisée en raison de l'imprécision de la détermination de l'âge, même si les estimations des âges ne sont pas biaisées. Nous avons mis au point une méthode par laquelle on peut connaître l'importance de ce biais d'après des renseignements sur la précision de la détermination de l'âge. Les simulations de Monte Carlo révèlent qu'il est possible de déterminer le biais avec exactitude. Nous avons constaté que l'estimation de Chapman–Robson, qui est couramment employée pour déterminer la mortalité, peut absorber l'imprécision de la détermination de l'âge lorsqu'on emploie toutes les classes d'âge. Toutefois, il est probable qu'il y ait des erreurs si l'on exclut une ou plusieurs classes d'âge ou si l'on emploie d'autres estimateurs pour déterminer la mortalité. Il est possible de corriger le biais si l'on connaît la distribution des erreurs des estimations de l'âge.

Received March 2, 1984
Accepted August 22, 1984
(J7709)

Reçu le 2 mars 1984
Accepté le 22 août 1984

Age–frequency distributions have frequently been used to estimate mortality rates via an application of stable population theory. Many methods have been proposed for extracting this mortality information from age distributions (Deevey 1947; Chapman and Robson 1960; Caughley 1966; Barlow 1982). All of these methods have assumed that ages could be determined without error. In fact, error in age estimation is a very real problem (Beamish and Fournier 1981; Chang 1982). Clearly, mortality rates could be biased if age estimation is biased. Here I address a slightly different question: can biased mortality estimates result from imprecise, but unbiased ages?

The assumptions required for estimating mortality rate (or its complement, survival rate) from age frequencies are stringent. Stated briefly, a population must be in stable age distribution and its growth rate must be known. These assumptions are treated in detail elsewhere (Caughley 1966; Barlow 1982). Despite stringent assumptions, use of these methods is common in fishery, marine mammal, and other wildlife research. The assumption of accurate age determinations has always been implicit, though usually unspoken.

Given a population with a zero growth rate, a stable age distribution, and a constant mortality rate with age, Chapman and Robson (1960) have derived a minimum variance, unbiased estimator of that population's survival rate based solely on sampled age frequencies. Because the Chapman–Robson (C–R) method is unbiased in cases where aging is deterministic, this method was chosen to examine potential biases when errors occur in age determination. Standard errors of the predicted survival rates can also be estimated from the C–R method.

The C–R survival rate estimator can be expressed in vector notation as

$$(1)\quad \hat{s} = \boldsymbol{n}\cdot\boldsymbol{v}' \Big/ \left(\sum_{i=1}^{\infty} n_i + \boldsymbol{n}\cdot\boldsymbol{v}' - 1\right)$$

where $\boldsymbol{n}$ is the vector of observed frequencies by age-class and $\boldsymbol{v}$ is a vector defined such that $v_i = i - 1$. This survival rate estimator can be reformulated in terms of two parameters: sample size and a scaled mean age (Chapman and Robson 1960, Eq. 4). It is trivial to show that an unbiased error in estimating ages will not affect the expected value of the scaled mean age. Imprecision in estimating ages will, therefore, not affect the expected value of C–R survival rate if all age-classes are included. Frequently the first several age-classes are excluded because their abundance cannot be estimated without bias (e.g. Barlow 1982, Chap. 1). The exclusion of the first age-classes can introduce a bias in the estimation of survival rates when age estimation is subject to errors. In this paper, I derive an expression that predicts the magnitude of this bias and use Monte Carlo simulations to verify the ability of this expression to predict bias accurately.

I only consider the special case for which age estimation is unbiased. In fact, there are few situations where the probability of counting too many annual layers would equal the probability of counting too few. It will be assumed that these types of errors can be corrected with calibration studies.

Methods

To remain consistent with the terminology of Chapman and Robson (1960) and common usage, ages and errors in ages are represented as discrete integers (days, years, etc.). The distribution of aging errors is seldom uniform over all ages. Most commonly, young animals can be aged with greater precision than older animals. The probability distribution of age estimates for a given age-class can be given as columns of a transition probability matrix (e.g. Table 1). The (i, j)th element of such a matrix, $\boldsymbol{P}$, would represent the probability that an individual in age-class j would be interpreted as belonging to age-class i. The product of the transition matrix times the true age distribution of a sample, $\boldsymbol{n}$, would thus give the age distribution that might be expected to be observed given $\boldsymbol{n}$, $\boldsymbol{m}$:

$$(2)\quad \boldsymbol{P}\cdot\boldsymbol{n} = \boldsymbol{m}.$$

The observed age distribution would be expected to differ from the true age distribution unless (trivially) $\boldsymbol{P}$ is the identity matrix, or (miraculously) $\boldsymbol{n}$ is an eigenvector of $\boldsymbol{P}$ with a unit eigenvalue.

When errors in aging are considered, the expected C–R survival rate could be estimated by substituting $\boldsymbol{m}$ for $\boldsymbol{n}$ in Equation 1:

$$(3)\quad \hat{s} = \frac{\boldsymbol{m}\cdot\boldsymbol{v}'}{\sum_{i=k}^{\infty} m_i + \boldsymbol{m}\cdot\boldsymbol{v}' - 1}$$

where k is the first age-class included in the estimation and $\boldsymbol{v}$ is defined such that $v_i = 0$ if $i \leqslant k$, and $v_i = i - k$ if $i > k$.

In this study, the expected value of $\hat{s}$ was calculated for a range of values of the actual survivorship ($s = 0.25$–0.75) and the first age-class to be included ($k = 1$–10). The expected age distribution of a sample was estimated as the geometric series corresponding to the true survivorship. The distribution of aging errors was determined by the probability transition matrix (Table 1). For all ages, the aging errors were symmetric about the true age; hence, the expected age of any individual would equal its true age. Biases due to aging errors were estimated as the difference between the survival rate calculated using Equations 2 and 3 and the true survival rate.

TABLE 1. Probability distributions of aging errors by age-class. Elements indicate the probability that an individual with a given true age will be assigned to the indicated categories of estimated age. Note that errors are symmetrically distributed about the principle diagonal within columns. Note also that aging precision is assumed constant for individuals older than 6.

Estimated age	True age																
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	·	·	·
1	1.0	0.1																
2		0.8	0.2	0.1	0.1	0.1												
3		0.1	0.6	0.2	0.1	0.1	0.1											
4			0.2	0.4	0.2	0.1	0.1	0.1										
5				0.2	0.2	0.1	0.1	0.1	0.1									
6				0.1	0.2	0.2	0.1	0.1	0.1	0.1								
7					0.1	0.1	0.2	0.1	0.1	0.1	0.1							
8					0.1	0.1	0.1	0.2	0.1	0.1	0.1	0.1						
9						0.1	0.1	0.1	0.2	0.1	0.1	0.1	0.1					
10						0.1	0.1	0.1	0.1	0.2	0.1	0.1	0.1	0.1				
11							0.1	0.1	0.1	0.1	0.2	0.1	0.1	0.1	0.1			
12								0.1	0.1	0.1	0.1	0.2	0.1	0.1	0.1	·	·	·
13									0.1	0.1	0.1	0.1	0.2	0.1	0.1			
14										0.1	0.1	0.1	0.1	0.2	0.1			
15											0.1	0.1	0.1	0.1	0.2			
·												·				·		
·												·					·	
·												·						·

Monte Carlo simulations were used to test the ability of the described procedures to estimate bias resulting from errors in age determinations. Age distributions were generated by randomly drawing discrete samples (with replacement) from a population with a geometric series distribution. This is analogous to a population with constant recruitment and with a survival rate that does not vary with age. In order to mimic error in age determination, a random integer was added to or subtracted from each age selected from the population. Again the distribution of errors was taken from Table 1.

For purposes of illustration, mean values of the C–R estimate were calculated from simulations using three different survival rates (0.3, 0.5, and 0.7) and three different starting ages (1, 2, and 3). These fall within the range of values used in the deterministic approach. The simulation was run with 1000 age distributions (with errors) for each of these nine permutations. Sample sizes for "aged" individuals of all age-classes were set so that the nominal sample for survival rate estimation was 200. Survival rates were only estimated for those individuals whose "apparent" age was greater than or equal to a given starting age (1, 2, or 3); hence, sample size varied slightly about this nominal value due to stochastic effects. Means and standard deviations of survival rates were calculated for each set of 1000 age distributions.

Results

The expected survival rate estimates from the C–R method are shown in Fig. 1 for a range of true survival rates and number of excluded age-classes. As predicted, the method is unbiased if all age-classes are included. If the initial age-class(es) are excluded, an appreciable bias can result. For the given error matrix, the magnitude of this bias is greater when survival rates are low and smaller when survival rates are high. When the first included age-class is 10 or greater, the bias disappears completely.

The results of the Monte Carlo simulation confirm these results. The average survival rates estimated using the C–R method are given in Table 2 for each of the nine combinations of true survival rates and starting ages. Each represents the average estimate from 1000 randomly selected age distributions with simulated error in age determination. Also tabulated are the survival rates predicted using Equations 2 and 3 and the expected (geometric series) age distributions. The magnitude of the bias observed in the simulations was in good agreement with the bias predicted from Equation 3. Observed standard errors in the survival rate estimates were only trivially different from those predicted by the C–R formulations (J. Barlow, unpubl. data).

Discussion

Age distributions typically resemble a declining exponential function. Errors in aging will usually change the shape of such a

TABLE 2. Results of Monte Carlo simulations of survival rate estimation with errors in age determinations. Mean survival rate estimates are averages of 1000 C–R estimates from randomly selected and transformed age distributions. Predicted survival rate estimates are from Equations 2 and 3, using a geometric series age distribution (corresponding to the actual survival rate) for n.

	First age-class included		
	1	2	3
s	0.3	0.3	0.3
Mean $\hat{s}$	0.2993	0.3492	0.3589
Predicted $\hat{s}$	0.3000	0.3490	0.3597
s	0.5	0.5	0.5
Mean $\hat{s}$	0.4995	0.5254	0.5452
Predicted $\hat{s}$	0.5000	0.5250	0.5446
s	0.7	0.7	0.7
Mean $\hat{s}$	0.6996	0.7079	0.7221
Predicted $\hat{s}$	0.7000	0.7090	0.7225

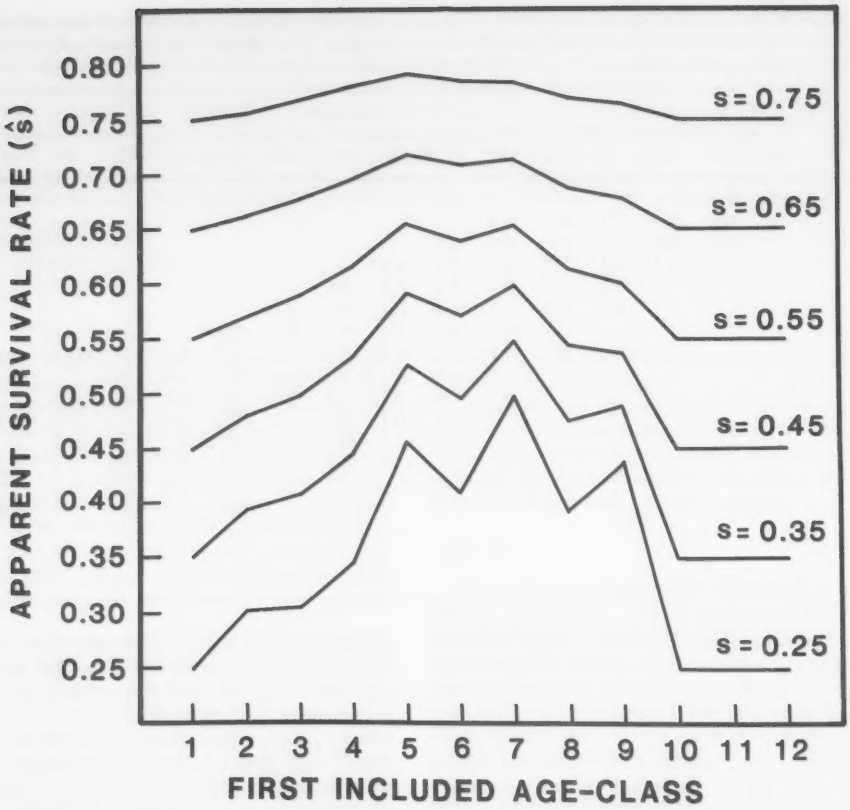

FIG. 1. Apparent survival rates from the C–R method as a function of the first age-class to be included in the estimation. Each line represents a different value of the true survival rate. Errors in age determination are as given in Table 1.

function. It is somewhat fortuitous that the C–R estimator is robust to such changes (if errors are unbiased and all age-classes are included). In the example used here, the method was also unbiased for age-classes 10 and greater. This age is the greatest possible "apparent" age corresponding to the true age at which aging precision becomes constant (Table 1). The C–R method is thus also unbiased in cases where aging precision does not vary with age.

The implications of these results go far beyond the simple examples given here. From information presented thus far, it would seem obvious that bias can be avoided by using the C–R estimator and including all age-classes for which age determination is imprecise. Unfortunately, this solution has a greater conceptual than practical value.

The C–R survival estimator is valid only in the special case where survival rates are constant with age. The decision to use this method is typically based on whether the observed age frequencies fit an expected geometric series age distribution. Robson and Chapman (1961) have formulated a stepwise test that allows the elimination of age-classes that do not meet this expectation. One problem is that errors in age estimation change the shape of the observed age–frequency distribution. Although the true age distribution of a sample may follow a geometric series, the observed distribution may be significantly different, and thus might result in a decision not to use the C–R method or to erroneously eliminate the first age-class(es).

To demonstrate this, Monte Carlo simulations were again used, with the first age-class being chosen by a stepwise chi-square test (Robson and Chapman 1961). Survival rates of 0.3, 0.5, and 0.7 were used, a simulated sample of 1000 aged individuals was drawn, and random errors were introduced in age estimates as before. Using the method of Robson and Chapman to determine the first age-class to be included, mean estimates of survival rates were 0.353, 0.532, and 0.715, respectively, for s = 0.3, 0.5, and 0.7, indicating an appreciable positive bias. Ironically, tests that are intended to avoid biases may introduce new biases.

A different problem exists if survival rates change with age: the C–R method is not valid. Most techniques for estimating age-varying survival rates depend on the slope of an age–frequency curve (Caughley 1966; Siler 1979; Barlow 1982, Chap. 2). Because errors in aging typically affect the shape of the observed age–frequency distributions (hence, their slopes), these methods will be biased even if all age-classes are included.

Bias in survival rate estimation resulting from aging errors is thus a complex problem. A general solution for all methods of survival rate estimation does not exist. For the C–R method, a simple approach can be used to estimate expected bias. This

approach can be visualized in Fig. 1. For a given error matrix, P, the true survival rate can be interpolated from this figure if the apparent survival rate and initial age-class are specified.

A similar, but more rigorous approach would be to calculate expected age–frequency distributions for a range of true survival rate values. These true-age distributions are then transformed by P to give estimated-age distributions. The probabilities that the observed age distribution could have been drawn from each of these estimated-age distributions are calculated, and $\hat{s}$ is estimated as the value corresponding to the transformed age distribution that maximizes this probability.

Acknowledgments

I thank D. Chapman, J. Cooke, D. DeMaster, T. Gerrodette, D. Goodman, A. MacCall, R. Methot, J. Pella, and S. Reilly for their helpful comments and suggestions.

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Predation by Rock Crabs (*Cancer irroratus*) on Diseased Sea Urchins (*Strongylocentrotus droebachiensis*) in Nova Scotia

Robert E. Scheibling

Department of Biology, Dalhousie University, Halifax, N.S. B3H 4J1

Scheibling, R. E. 1984. Predation by rock crabs (*Cancer irroratus*) on diseased sea urchins (*Strongylocentrotus droebachiensis*) in Nova Scotia. Can. J. Fish. Aquat. Sci. 41: 1847–1851.

Predation of morbid sea urchins (*Strongylocentrotus droebachiensis*) by rock crabs (*Cancer irroratus*) and other predators was observed using SCUBA during an outbreak of disease in southwestern Nova Scotia in August 1983. Disease increases susceptibility of sea urchins to predation by precluding natural defensive behaviors including spine projection, strong attachment to the substratum, and aggregation. In laboratory feeding experiments, rock crabs preferred diseased or narcotized sea urchins over healthy ones and fed upon them at a much higher rate than crabs given only healthy sea urchins as prey. Rock crabs showed no significant preference between diseased and narcotized sea urchins. Rock crabs clearly preferred mussels over healthy or diseased sea urchins. Although rock crabs do not appear to be important predators of healthy sea urchins, from field and laboratory findings I conclude that they contribute to mass mortality of sea urchins by preying upon morbid individuals during outbreaks of disease.

Nous avons étudié la prédation des oursins *Strongylocentrotus droebachiensis* par le crabe *Cancer irroratus* et d'autres prédateurs en effectuant des observations en plongée sous-marine pendant qu'une maladie frappait les oursins dans le sud-ouest de la Nouvelle-Écosse en août 1983. La maladie fait de l'oursin une proie plus facile en l'empêchant de recourir à ses mécanismes de défense naturels qui consistent notamment à hérisser ses épines, à s'accrocher au substrat et à se rapprocher de ses congénères. Dans des expériences effectuées en laboratoire, nous avons constaté que les crabes s'attaquent aux oursins malades ou traités au narcotique de préférence aux sujets sains, et qu'ils en mangent beaucoup plus que les crabes auxquels on ne donne que des oursins sains. Les crabes n'ont pas manifesté de préférence significative pour les oursins malades ou pour les oursins traités au narcotique, mais ils préféraient nettement les moules aux oursins, malades ou sains. Bien qu'ils ne semblent pas s'attaquer dans une importante mesure aux sujets sains, ils sont néanmoins la cause d'une mortalité massive chez les oursins, car ils chassent ceux qui sont malades.

Received May 8, 1984
Accepted August 22, 1984
(J7780)

Reçu le 8 mai 1984
Accepté le 22 août 1984

Major transitions in the rocky subtidal community off the Atlantic coast of Nova Scotia are mediated by the population dynamics of sea urchins, *Strongylocentrotus droebachiensis* (Scheibling 1984). In the early 1970's, destructive grazing by expanding populations of sea urchins transformed luxurient kelp beds into sea urchin dominated barren grounds in St. Margarets Bay (Breen and Mann 1976). Mann and co-workers proposed that predators are important in controlling sea urchin populations and that a reduction in predation pressure may underlie sea urchin population explosions (see Mann 1977, 1982 for review).

Rock crabs, *Cancer irroratus*, are known to be a predator of *S. droebachiensis* although their predatory impact on sea urchin populations remains unclear. Sea urchin remains are infrequently found in the guts of rock crabs in the wild (Scarratt and Lowe 1972; Drummond-Davis et al. 1982). Predation rates of about 1 sea urchin·crab^{-1}·d^{-1} have been recorded in laboratory studies although rock crabs show a clear preference for mussels, *Mytilus edulis*, when offered a choice (Himmelman and Steele 1971; Elner 1980; Drummond-Davis et al. 1982). Arguments both for and against the importance of rock crabs in controlling sea urchin populations have been made on the basis of laboratory feeding studies (Elner 1980; Drummond-Davis et al. 1982). Bernstein et al. (1981) proposed that rock crab and lobster predation retains sea urchins at low density and in hiding in kelp beds. However, at higher sea urchin densities the presence of predators may facilitate the formation of aggregations of sea urchins which may destructively graze kelp (Bernstein et al. 1981, 1983).

In recent years, widespread outbreaks of disease in *S. droebachiensis* have occurred along the Atlantic coast of Nova Scotia (Miller and Colodey 1983; Scheibling and Stephenson 1984; Scheibling 1984). This study was undertaken to document predation by rock crabs and other predators upon morbid sea urchins during these epizootics and to examine the basis for the increased susceptibility of diseased sea urchins to predation.

Materials and Methods

Predator–prey interactions between *C. irroratus* and *S. droebachiensis* were investigated using SCUBA at Eagle Head, Nova Scotia (station 1, Scheibling and Stephenson 1984) between June and October 1983. The study area was a nearshore trough of small cobble encrusted with coralline algae (*Lithothamnion* sp., *Clathromorphum* sp., *Phymatolithon* sp.) at 3–4 m depth. Rock crab and sea urchin densities were measured in 15 randomly located 0.25-m^2 quadrats within a 4 × 50 m (200 m^2) grid. Crabs feeding on sea urchins, and recently killed sea urchins (with spines still attached), were enumerated and measured within the entire grid. Crab size was measured as carapace width; sea urchin size was measured as horizontal test diameter. Attraction of crabs to injured sea urchins was investigated by cutting large sea urchins (40–50 mm) in half and monitoring subsequent activity of crabs.

For laboratory experiments, sea urchins and rock crabs were freshly collected by divers at Eagle Head and Halifax Harbour, respectively, in June 1983. Mussels (*M. edulis*) were obtained from cultures in the Department of Biology, Dalhousie University. Crabs were divided into two groups of five individuals, ranging in size from 60 to 100 mm. Only male or nonberried female crabs were used. Individual crabs were maintained in 50 × 50 cm fiberglass tanks, filled with running seawater to a depth of 20 cm. They were exposed to a 12 h light : 12 h dark cycle and ambient seawater temperatures ranging from 8 to 15°C during experiments.

TABLE 1. Daily variation in predation of sea urchins (*S. droebachiensis*) by crabs (*C. irroratus*) in a 200-m^2 area at Eagle Head, Nova Scotia.

Date	Time	Number of crabs feeding on urchins	Number of recently killed urchins[a]
Aug. 17	12:00	11	28
Aug. 23	12:00	13	71
	18:00	7	14
	24:00	0	2
Aug. 24	12:00	8	25

[a]Recently killed sea urchins were removed during each sampling.

Individual crabs of each group were given 16 prey items daily in three series of experiments: (1) crabs given equal numbers of diseased and healthy sea urchins (group 1) or only healthy sea urchins (group 2); (2) crabs given equal numbers of narcotized sea urchins and diseased (group 1) or healthy (group 2) sea urchins; and (3) crabs given equal numbers of mussels and diseased (group 1) or healthy (group 2) sea urchins.

Diseased sea urchins were obtained by exposing healthy individuals to diseased conspecifics as described by Scheibling and Stephenson (1984). Narcotized sea urchins were obtained by placing healthy sea urchins twice daily (09:00 and17:00) in an isotonic solution of MgCl in water (72 g·L^{-1}) for 20 min. This treatment inactivated individuals for 6–8 h but allowed complete recovery. Narcotized sea urchins were dyed with two or three drops of a 5% solution of Nile Blue (Fisher) applied to the peristomial membrane. The vital stain was discernable for about a week. In preliminary experiments, two crabs each given eight dyed and eight nondyed narcotized sea urchins for 10 d showed no feeding preference (mean ratio of dyed to nondyed sea urchins consumed = 1.11, $N = 49$).

In each feeding experiment the number and type of prey consumed per crab were recorded daily for 1 or 2 wk. Consumed prey were replaced and unconsumed test/shell fragments were removed. Unconsumed diseased sea urchins were replaced regularly; only individuals at an early stage of morbidity were used. Prey size ranged from 30 to 40 mm (horizontal test diameter for sea urchins, shell length for mussels). Crabs were starved for 1 wk prior to each series of feeding experiments to standardize hunger level.

Results

On August 17 and 23, 1983, *S. droebachiensis* at Eagle Head showed initial symptoms of disease, including flaccid and retracted tube feet, flattened and disheveled spines, gaping mouth and jaws, and weak to no attachment to the substratum. A random sample of 20 sea urchins also had empty guts and flecks of purplish pigmentation on the inner surface of the test indicating concentrations of coelomocytes. Sea urchins in late stages of morbidity (extensive spine loss, epidermal necrosis) were not observed at this time. Sea urchin density was 50.9 ± 36.6 individuals·m^{-2}.

During this outbreak of disease, *C. irroratus* were abundant (density increased from 0.8 ± 1.6 individuals·m^{-2} on June 10 to 3.7 ± 1.6 individuals·m^{-2} on August 17) and preyed on

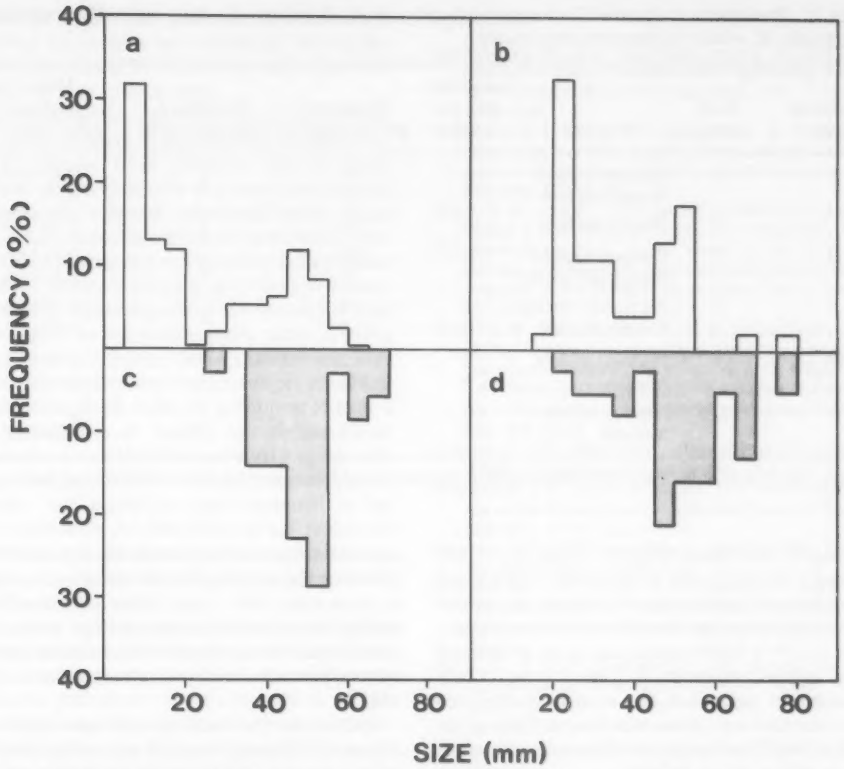

FIG. 1. Size frequency distributions of *S. droebachiensis* and *C. irroratus* at Eagle Head, August 17–23, 1983. (a) Sea urchin population ($N = 191$); (b) rock crab population ($N = 46$); (c) sea urchins preyed upon by rock crabs ($N = 35$); (d) rock crabs preying upon sea urchins ($N = 38$).

morbid sea urchins. Crabs fed on sea urchins mainly during the day; none were feeding at midnight (Table 1). The rate of sea urchin mortality due to crab predation, estimated as the number of urchins consumed or being consumed over a 24-h period (August 23–24, Table 1) was 0.25 individuals$\cdot m^{-2} \cdot d^{-1}$ or about 0.5% of the sea urchin population (on August 17) per day. Crabs that fed on sea urchins were among the largest individuals of the crab population; their prey were among the largest of the sea urchin population (Fig. 1). There was no correlation between the size of a crab feeding on a sea urchin and the size of its prey (Spearman's rank correlation test, $P > 0.20$).

Cancer irroratus attacking morbid sea urchins generally overturned their prey with their chelae and walking legs, and then punctured the peristomial membrane around the mouth with a chela and removed the jaws and teeth (Aristotle's lantern). This opening often was enlarged by chipping off and discarding fragments of the test surrounding the peristome with the chelae. Soft tissues (primarily gut and gonad) were picked out of the test. Tests of small urchins often were cracked in half.

Lobsters (*Homarus americanus*) were observed preying upon morbid sea urchins on two occasions at night. The lobsters cracked the sea urchins in half with their large crusher chelae and ingested the soft tissues using their mouth parts. Whelks (*Buccinum undatum*) were observed on four occasions scavenging pieces of sea urchin test. Starfish (*Asterias vulgaris, Henricia sanguinolenta*) were rare at Eagle Head in 1983, but occasionally were observed scavenging morbid sea urchins during a previous epizootic in 1982.

Sea urchins that were cut in half by divers readily attracted crabs over a 1- to 3-m radius. In 10 trials on August 23, one or more crabs entered a 10-cm radius around a dissected sea urchin in a mean (±SD) time of 48 (±31) s (range = 15–100 s). Crabs of all sizes converged on the bait. Small crabs yielded to larger ones; larger crabs of similar size fought for possession of the prey. Up to eight crabs collected about the bait but usually only one fed at a time. A lobster and a whelk also were attracted to the bait. Sea urchin tests were cleaned of soft tissues in 6–25 min. Test fragments were not consumed. Sea state was calm with little wave surge, and visibility was about 5 m during all trials.

A mass mortality of *S. droebachiensis*, attributed to disease, occurred sometime between August 24 and September 8, 1983. On September 8, there were no surviving sea urchins. Sea urchin tests littered the bottom (mean ± SD density = 47 ± 46 tests$\cdot m^{-2}$); almost all were without spines, many were completely intact (i.e. with no sign of crab predation). In the laboratory, freshly killed sea urchins lost all their spines in 4–6 d. Therefore, the mass mortality probably occurred over a period of about a week in late August – early September. Large *C. irroratus* disappeared from the study area after the mass mortality of sea urchins although rock crab density remained high due to the appearance of numerous small crabs (carapace width < 15 mm) in the quadrat samples (5.1 ± 5.1 individuals$\cdot m^{-2}$, October 22).

The results of laboratory feeding experiments are given in Table 2. *Cancer irroratus* given equal numbers of diseased and healthy sea urchins fed exclusively upon diseased ones and

TABLE 2. Predation by rock crabs (*C. irroratus*) on healthy, diseased, and narcotized sea urchins (*S. droebachiensis*) and mussels (*M. edulis*) in laboratory experiments.

Experiment series	Crab group	Prey type	Available prey per crab	Number of prey consumed	Duration of experiment (wk)	Mean (±SD) predation rate (prey·crab^{-1}·d^{-1})
I	1	Diseased urchins	8	33	2	0.47 (±0.19)
		Healthy urchins	8	0		0
	2	Healthy urchins	16	11	2	0.16 (±0.13)
II	1	Diseased urchins	8	29	2	0.41 (±0.34)
		Narcotized urchins	8	17		0.24 (±0.19)
	2	Narcotized urchins	8	55	2	0.79 (±0.39)
		Healthy urchins	8	2		0.03 (±0.06)
III	1	Diseased urchins	8	2	1	0.06 (±0.12)
		Mussels	8	113		3.23 (±0.84)
	2[a]	Healthy urchins	8	0	1	0
		Mussels	8	80		3.20 (±0.42)

[a]One crab molted at the start of the experiment; it did not feed and was excluded from calculation of feeding rate.

at a significantly higher rate (Mann Whitney *U*-test, $P = 0.01$) than crabs provided with healthy sea urchins only. Crabs given equal numbers of diseased and narcotized, healthy sea urchins consumed more diseased ones but the difference was not statistically significant (χ^2, $P > 0.05$) (mean ratio ± SD of diseased to narcotized sea urchins consumed = 1.66 ± 0.54). Crabs given equal numbers of narcotized and normal, healthy sea urchins fed almost exclusively on narcotized ones. Crabs given equal numbers of mussels and healthy, or diseased, sea urchins fed exclusively, or almost so, on mussels.

Healthy sea urchins generally clustered along the sides of tanks in groups of two to eight individuals but were always accessible to crabs due to the shallow depth of the tanks. Diseased or narcotized sea urchins lay unattached and inactive on the bottom of the tank. Individuals narcotized at 17:00 recovered completely before being narcotized again at 09:00 of the next day.

Crabs manipulated diseased and narcotized sea urchins with their chelae and walking legs. The chelae were used to crack the test, often by insertion through the peristomial membrane. The chelae and mouth parts were used to extract and ingest soft tissues from fragments of the broken test. There was no correlation between crab size and feeding rate in any of the experiments.

Group 1 of *C. irroratus* always was given diseased sea urchins whereas group 2 never was given them. Although crabs in group 1 consumed an average of 13 diseased sea urchins per crab during the feeding experiments, they showed no signs of morbidity or abnormal behavior either during the experiments or during a subsequent 2-mo period of observation.

Discussion

Possibly, the marked increase in abundance of *C. irroratus* in the study area between June and August 1983 was related to the increase in morbid *S. droebachiensis* as prey. However, rock crab density generally increases in nearshore areas in summer (R. W. Elner, DFO, Biological Station, St. Andrews, N.B., pers. comm.). Initial predation of morbid sea urchins by local crabs may have attracted other crabs from neighboring areas. Baiting experiments indicated that crabs are readily attracted to injured sea urchins. Large crabs disappeared from the study area following the catastrophic die-off of sea urchins due to disease in September 1983. Rock crabs occasionally were observed feeding on morbid sea urchins during a previous epizootic in the fall of 1982. However, there was no evidence of crab predation upon apparently healthy survivors between January and July 1983.

Rock crabs generally preyed upon adult sea urchins (test diameter > 20 mm). Juvenile sea urchins tended to occur on the undersides and interstices of the cobble and may have had a spatial refuge from predation. Juvenile rock crabs (carapace width < 20 mm) also occurred under the cobble but were not observed preying upon sea urchins. Baiting experiments indicated that a number of crabs may feed in succession on a single sea urchin. Thus, small crabs may scavenge the remains of relatively large sea urchins initially attacked by large crabs. This may account in part for the lack of correlation between crab size and sea urchin size in feeding observations.

In laboratory feeding experiments *C. irroratus* showed a clear preference for morbid sea urchins over healthy ones. Predation rate on healthy urchins was low, even when they were the only prey available. Experiments with narcotized sea urchins suggest that preference for morbid sea urchins is related to the inactivation of physical defence mechanisms. Crabs attacking healthy sea urchins usually detach the prey from the substratum and overturn it to gain access to the vulnerable peristomial membrane (Himmelman and Steele 1971; Elner 1980; this study). Healthy sea urchins may aggregate, rendering themselves more resistent to manipulation than lone individuals (Garnick 1978; Bernstein et al. 1981). In contrast, morbid or narcotized sea urchins have no attachment or mobility and they are easily manipulated and overturned by crabs. In morbid sea urchins, a loss of tube foot and spine function arises from the breakdown of muscle tissue syptomatic of the disease (Jones et al. 1985). Given a choice, crabs appeared to prey more on morbid sea urchins than on narcotized ones. Although the difference was not statistically significant, it may be due in part to the recovery of narcotized individuals each night during the experiments.

The clear preference of rock crabs for mussels over healthy sea urchins is consistent with previous findings (Elner 1980;

Drummond-Davis et al. 1982). The preference for mussels is retained when morbid sea urchins are substituted for healthy ones, suggesting that sea urchins, even in a weakened condition, are not a highly favored prey of rock crabs.

Mortality of *S. droebachiensis* due to crab predation at Eagle Head in 1983 was minor relative to the catastrophic die-off of sea urchins due to disease. Crab predation may be more important during less severe outbreaks of disease by reducing the number of chronically infected individuals which might otherwise recover. Crabs also may contribute to the total elimination of the sea urchins during major epizootics. In September 1983, rock crabs were observed preying upon the few chronically infected sea urchins remaining after mass mortalities near Liverpool and Lockeport on the southwestern shore of Nova Scotia. Other invertebrates, including lobsters and starfish, may augment or replace rock crabs as important predators of morbid sea urchins in other areas. Rock crabs do not appear to have a major impact on populations of healthy sea urchins. Crab predation on sea urchins was only observed during epizootics. Crabs show a very low preference for healthy sea urchins in feeding experiments, and predation rates measured in the laboratory are low relative to the abundance of sea urchins in nature. Studies of rock crab gut contents also suggest that sea urchins are a minor component of their diet (Scarratt and Lowe 1972; Drummond-Davis et al. 1982).

Rock crabs and other predators/scavengers of morbid sea urchins are apparently unaffected by the disease of sea urchins. A parasitic amoeba (*Paramoeba* sp.) found in tissues of diseased sea urchins may be the pathogenic agent (Jones et al. 1985). Interestingly, a similar microorganism (*Paramoeba pernisciosa*) has been identified as a parasite causing mass mortality in the blue crab (*Callinectes sapidus*) (Johnson 1977).

Acknowledgements

I thank Tracy Willar, Bruce Raymond, and Stewart Johnson for technical assistance and Drs. R. W. Elner and P. Brunel for critically reviewing the manuscript. This research was supported by grants from the Department of Fisheries and Oceans and the Natural Sciences and Engineering Research Council of Canada.

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Role of Fish in Regulation of Plant and Animal Communities in Eutrophic Ponds[1]

Craig N. Spencer and Darrell L. King

Department of Fisheries and Wildlife, Michigan State University, East Lansing, MI 48824-1222, USA

Spencer, C. N., and D. L. King. 1984. Role of fish in regulation of plant and animal communities in eutrophic ponds. Can. J. Fish. Aquat. Sci. 41: 1851–1855.

Alteration of fish communities resulted in marked changes in the zooplankton, phytoplankton, and benthic plant communities in nutrient-rich ponds. In ponds containing dense populations of fathead minnows (*Pimephales promelas*) and brook sticklebacks (*Culaea inconstans*), intense fish predation resulted in sparse cladoceran zooplankton populations and turbid water dominated by dense blue-green algal blooms. In ponds containing no fish, or dense populations of largemouth bass (*Micropterus salmoides*), abundant Cladocera reduced phytoplankton densities through heavy grazing, and these ponds

[1]Michigan Agricultural Experiment Station journal article No. 10629.

were characterized by clear water and dense growths of *Elodea canadensis*, *Potamogeton* spp., and *Cladophora* sp. Manipulation of fish populations to control unwanted algal blooms in shallow eutrophic lakes may yield dense growths of equally undesirable macrophytes and periphyton.

Nous avons constaté que dans des étangs riches en éléments nutritifs, le zooplancton, le phytoplancton et les plantes benthiques avaient subi des changements marqués par suite d'une modification des communautés de poissons. Dans les étangs densément peuplés de têtes-de-boules (*Pimephales promelas*) et d'épinoches à cinq épines (*Culaea inconstans*) la prédation par les poissons était intense, si bien que les cladocères se sont raréfiés et que les algues bleues ont proliféré dans les eaux devenues troubles. Dans les étangs ne contenant aucun poisson ou une forte population d'achigans à grande bouche (*Micropterus salmoides*), les cladocères abondaient et la phytoplancton s'est amenuisé sous l'effet de leur broutage ; les eaux de ces étangs étaient limpides et l'on pouvait y voir des colonies denses d'*Elodea canadensis*, de *Potamogeton* spp. et de *Cladophora* sp. La modification des populations de poissons en vue de prévenir la prolifération des algues dans les lacs eutrophes peu profonds peut provoquer la prolifération de macrophytes et d'organismes du périphyton tout aussi nuisibles.

Received February 21, 1984
Accepted August 17, 1984
(J7696)

Reçu le 21 février 1984
Accepté le 17 août 1984

The role of fish in regulating lake ecosystems remains underestimated in spite of a growing number of studies demonstrating their importance. Over 20 yr ago, Hrbacek et al. (1961) showed that alteration of fish populations in two reservoirs in Czechoslovakia resulted in profound changes in the zooplankton and phytoplankton communities and suggested that biological factors were at least as important as chemical and physical factors in regulating aquatic ecosystems. Since then, a number of studies have demonstrated the potential importance of upper trophic levels in control of algae in lakes (Grygierek et al. 1966; Hurlbert et al. 1972; Losos and Hetesa 1973; Andersson et al. 1978; Shapiro 1980; Lynch and Shapiro 1981; Hurlbert and Mulla 1981). Despite these studies, the primary research focus remains devoted to the role of plant nutrients, particularly phosphorus, in determining lake conditions (Vollenweider 1968; Dillon and Rigler 1974; Jones and Bachmann 1976; Schindler 1978). Although such nutrients are the primary drivers determining the level of fertility, our purpose was to quantify fish-induced alterations in the zooplankton and algal communities as well as concomitant changes in the submerged macrophyte community, an area that has received little quantification to date.

Study Site and Methods

We examined the role of piscivorous fish, largemouth bass (*Micropterus salmoides*), and two planktivorous fish, fathead minnows (*Pimephales promelas*) and brook sticklebacks (*Culaea inconstans*), in regulating the zooplankton, phytoplankton, periphyton, and submerged macrophyte communities in shallow, nutrient-rich ponds. This research was conducted at the Inland Lakes Research and Study Center located on the campus of Michigan State University. This facility consists of four ponds ranging in size from 3.3 to 5.0 ha, each with a depth of 1.8 m. The ponds were filled with nutrient-rich, secondary effluent from the East Lansing, Michigan, Wastewater Treatment Plant. Phosphorus levels were maintained in the range of highly enriched waters, with orthophosphorus concentrations remaining above 0.1 mg PO_4-P/L in all four ponds.

A preliminary study was conducted in 1979, followed by an in-depth study from April through September 1980. Phytoplankton were sampled weekly with a tubular water sampler yielding integrated samples of the entire water column. Phytoplankton were enumerated with a compound microscope at 400× using the membrane filtration technique described by McNabb (1960). Zooplankton were sampled weekly with an 80-μm-mesh plankton net using oblique tows spanning the entire water column. Zooplankton were enumerated in a gridded dish using a dissecting microscope. Macrophytes and periphyton were sampled monthly with an Eckman dredge. Plants were washed, sorted, and dried to constant weight at 105°C. Planktivorous fish densities were estimated in September 1980 using an 18-m-long, 6-mm-mesh bag seine. Largemouth bass densities were estimated in pond 4 from counts of dead fish following their elimination with rotenone in April 1981. Water samples for chemical analysis were collected weekly with a Kemmerer sampler from a depth of 1 m. Analyses for orthophosphorus, total phosphorus, nitrate, nitrite, ammonia, and alkalinity were made with a Technicon Auto Analyser II. Vertical profiles of dissolved oxygen, pH, light penetration, and water temperature were made weekly with calibrated field meters. Detailed chemical and physical data are presented in Spencer (1981).

Results and Discussion

Prior to 1979, fish were not present in pond 2, which was characterized by clear water and dense growths of submerged macrophytes and periphyton exceeding 600 g dry wt/m^2, dominated by *Elodea canadensis* and *Cladophora* sp. (Burton et al. 1979). Small numbers of fathead minnows and brook sticklebacks were noticed for the first time in this pond in the spring of 1979, probably introduced by a mechanical aquatic weed harvester that was moved from pond to pond the previous summer. By late June, dense schools of juvenile planktivorous fish were observed throughout pond 2. Following the fish introduction, substantial changes occurred in the pond ecosystem (Fig. 1). Prior to the proliferation of planktivorous fish, the zooplankton were dominated by large filter-feeding Cladocera, primarily *Daphnia pulex*. Following the appearance of planktivorous fish, the Caldocera were replaced by copepods dominated by *Cyclops* sp., which in turn were replaced by rotifers dominated by *Keratella* sp. and *Brachionus* sp. This zooplankton progression, in a single summer season, supports size-selective predation and the size efficiency hypothesis (Brooks and Dodson 1965).

Soon after the decline of large filter-feeding Cladocera, the density of phytoplankton increased substantially and remained elevated for the remainder of the season (Fig. 1). Light penetration was greatly reduced as a result of the increased phytoplankton standing crop, with Secchi disc measurements falling to 0.5 m. Under these turbid water conditions, growth of

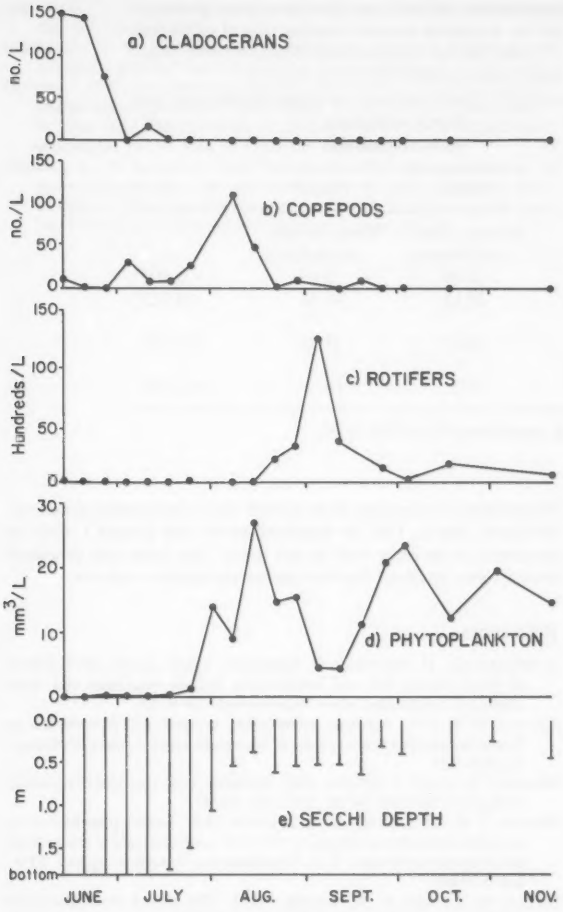

FIG. 1. Time course measurements of the density of (a) cladocerans, (b) copepods, (c) rotifers, (d) phytoplankton cell volume, and (e) Secchi depth in pond 2 during 1979 following the introduction of planktivorous fish.

submerged macrophytes and periphyton was limited severely, reaching a maximum seasonal biomass of 60 g dry wt/m^2, less than 10% of the maximum recorded the previous year.

The obvious shifts in zooplankton and plant dominance in pond 2 could not be attributed to changes in chemical parameters, since 1979 data for orthophosphorus, total phosphorus, nitrate, nitrite, and ammonia were similar to values reported in previous years in pond 2 (Burton et al. 1979; Spencer 1981). Apparently, the introduction of planktivorous fish resulted in the observed changes in species composition and abundance of zooplankton, algae, and macrophytes. Therefore, our in-depth study utilizing all four ponds was conducted the following year.

The 1980 study was initiated with pond 1 containing no fish, although in August small numbers of fathead minnows and brook sticklebacks found their way into the pond. Ponds 2 and 3 contained dense populations of fathead minnows and brook sticklebacks estimated in September 1980 at 25 000 and 1000/ha, respectively, in pond 2 and 13 000 and 58 000/ha in pond 3. The total length of these fish ranged from 50 to 90 mm. Pond 4 contained a dense population of largemouth bass estimated at 3000/ha. Over 99.9% of the bass were greater than 200 mm in total length, and these large piscivores maintained extremely low densities of smaller planktivorous fish. Although minnows and sticklebacks had been observed in pond 4 in previous years, we found none during this study. Stomach analyses of bass from pond 4 indicated that their diet consisted primarily of benthic macroinvertebrates including Odonata larvae, chironomid larvae, and snails.

Whereas all four ponds produced heavy growths of macrophytes or algae in 1980, our results clearly showed that fish–zooplankton interactions shifted the dominant plant type in these shallow, nutrient-rich ponds (Table 1). Ponds 1 and 4 with little or no planktivorous fish predation supported high densities of Cladocera, dominated by *Daphnia pulex* and *Ceriodaphnia* sp. By contrast, intense predation by planktivorous fish in ponds 2 and 3 yielded extremely low densities of Cladocera. Stomach analyses of fish from ponds 2 and 3 indicated that in the absence of Cladocera their diet consisted primarily of chironomid larvae and detritus. Intense grazing by Cladocera in ponds 1 and 4 resulted in low densities of phytoplankton dominated by pennate diatoms, small green algae, and flagellates. Blue-green algae were rarely found in ponds 1 and 4. Ponds 2 and 3, which were generally free from cladoceran grazing, maintained dense phytoplankton populations dominated by blue-green algae as high as 155 mm^3/L in late summer. These blooms were composed primarily of *Anabaenopsis Elenkinii* and *Microcystis* sp. Both of these algae contain gas vacuoles, and the resulting blooms were buoyant.

Light penetration was high in ponds 1 and 4 as a result of the low phytoplankton densities (Table 1). With abundant light available, ponds 1 and 4 supported dense growths of submerged macrophytes and periphyton over the entire pond bottom (Table 1), dominated by *Elodea canadensis*, *Potamogeton foliosus*, *Potamogeton crispus*, and *Cladophora* sp., which often extended to the pond surface. Submerged macrophyte and periphyton growth in ponds 2 and 3 was severely limited by poor light penetration and was restricted to the shallow zone near the shore.

Qualitative observations of bird and mammal populations in the ponds indicated that they too were affected by the different fish communities. Ponds 1 and 4 contained large breeding populations of mallards (*Anas platyrhynchos*) and muskrats (*Ondatra zibethica*), which made heavy use of the dense macrophyte growths in these ponds. Mallards and muskrats were infrequently observed in ponds 2 and 3; however, fish-eating birds including belted kingfishers (*Ceryle alcyon*), great blue herons (*Ardea herodias*), green herons (*Butorides striatus*), and snowy egrets (*Egretta thula*) were often observed in these ponds. These birds were commonly seen feeding on the plentiful small fish populations present in ponds 2 and 3, in contrast with ponds 1 and 4 where small fish and fish-eating birds were rarely found.

The absence of blue-green algal blooms in ponds 1 and 4 with abundant Cladocera was not due to removal of blue-green algae via cladoceran grazing. Blue-green algae are not considered a preferred food item for Cladocera (Hall 1964; Arnold 1971; Porter 1977), and we found no evidence that Cladocera ingested blue-green algae. Elevated light intensities (>20–50 $\mu E \cdot m^{-2} \cdot s^{-1}$) are known to result in negative buoyancy of gas vacuolate blue-green algae (Walsby and Booker 1980; Konopka 1982). Light intensities at the bottom of ponds 1 and 4 were frequently measured in excess of 100 $\mu E \cdot m^{-2} \cdot s^{-1}$ during the 1980 study. Under these conditions the formation of blue-green algal

TABLE 1. 1980 seasonal means of cladoceran density, phytoplankton cell volume, percent incident photosynthetically active radiation (PAR) reaching the pond bottom, and the maximum seasonal standing crop of submerged macrophytes and periphyton in the four experimental ponds. *P* values indicate significant differences between ponds without planktivorous fish (ponds 1 and 4) and ponds with dense planktivorous fish (ponds 2 and 3).

	Ponds without planktivorous fish		Ponds with dense planktivorous fish		
Measured variables	Pond 1	Pond 4	Pond 2	Pond 3	*P*
Fish community	No fish	Bass	Minnows and sticklebacks	Minnows and sticklebacks	
Cladocera (no./L)	24.72	34.99	0.06	0.03	<0.001[a]
Phytoplankton (mm^3/L)	2.58	7.39	20.13	36.18	<0.025[a]
Light penetration (% PAR at bottom)	17.39	10.94	0.45	0.25	<0.05[a]
Macrophytes and periphyton (g dry wt/m^2)	196	264	3	75	<0.05[b]

[a]ANOVA, split plot, repeat measurement design using log transformed data (Gill 1978).
[b]Student's *t*-test (one-sided).

blooms was likely prevented by reduced algal buoyancy (C. N. Spencer and D. L. King, unpubl. data).

In the study ponds, the type of dominant plant community was shifted readily from one form to another through alteration of the fish and zooplankton communities. Regardless of the status of the fish or zooplankton populations, however, abundant plant growth of some type always occurred in these nutrient-rich ponds. We suggest that manipulation of fish communities to control nuisance algal blooms (Hurlbert et al. 1972; Shapiro et al. 1975; Shapiro 1980) may not be successful in shallow lakes. Although undesirable phytoplankton densities may be reduced with this technique, subsequent increased growths of submerged macrophytes and periphyton such as we observed may be equally undesirable. While others have suggested the potential for increased growth of macrophytes as a result of fish manipulations (Hurlbert et al. 1972; Hrbacek and Dvorakova 1965), our study appears to be the first to actually quantify the shift from phytoplankton to macrophytes and periphyton. Manipulation of fish populations may offer the best potential for success in deep, steep-sided lake basins where much of the lake bottom lies below the photic zone, thereby reducing the potential for merely shifting plant production from phytoplankton to macrophytes and periphyton.

Fish, occupying the upper echelons of the food web, account for only a small amount of the total energy processed, and their role in pond or lake dynamics often is underestimated. Within the nutrient-rich ponds used in this study, fish-induced alterations of dominant plant type changed the entire ecology of the ponds. When planktivorous fish densities were low, mallards and muskrats made heavy use of the resulting abundant macrophytes and periphyton. Replacement of macrophytes and periphyton by dense algal blooms associated with control of the zooplankton by an abundance of planktivorous fish resulted in decreased use by muskrats and ducks and increased use by fish-eating birds including kingfishers, herons, and egrets. Thus, despite their presumed modest role in the total energy budget, fish populations can dictate characteristics of shallow, nutrient-rich ponds or lakes ranging from general appearance and water clarity to type and abundance of bird and animal use.

Acknowledgments

This research was supported by a grant from the Office of Water Research and Technology of the United States Department of Interior. We thank John L. Gill for statistical advice and Donald J. Hall for comments on an early draft of this paper. The paper also benefitted from reviews by Stuart Hurlbert and an anonymous reviewer.

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LETTERS AND COMMENTS/LETTRES ET COMMENTAIRES

Hypolimnetic Aeration and Zooplankton Depth Distribution

In a recent *Journal* paper, Taggart (1984) discussed the effect of hypolimnetic aeration on zooplankton depth distribution and concluded that the development of a stable anoxic metalimnion may preclude the development of the zooplankton food resource and therefore thwart the effectiveness of hypolimnetic aeration for restoring or enhancing cold-water fish production. I believe there are several inconsistencies in Taggart's (1984) experimental design and conclusions that require further explanation.

The main result of Taggart's (1984) experiment was that "in spite of aerator-induced hypolimnetic [O_2] to >4 mg/L for extended periods, virtually all crustacean plankton populations were restricted to the epilimnion during summer stagnation." However, the seasonal oxygen isopleths in Tory Lake (Taggart 1984, fig. 1) were similar to that seen in unaerated dimictic eutrophic lakes, i.e. temporary hypo- and meta-limnetic anoxia during summer and winter stratification (Wetzel 1983). This suggests that the aeration system had little effect on hypolimnetic oxygen concentrations. As a result, the observed zooplankton behaviour (i.e. avoidance of the hypolimnion, confinement to the epilimnion, and subsequent size-selective predation by fathead minnows) may have been unrelated to the experimental treatment.

Hypolimnetic aeration, when correctly designed, significantly increases hypolimnetic oxygen concentrations (Fast 1971; Ashley 1983a) and provides suitable habitat for cold-water fish and zooplankton (Overholtz et al. 1977; Ashley 1983b). The development of an anoxic metalimnion, which is a natural occurrence in certain lakes (Wetzel 1983), should not reduce the effectiveness of hypolimnetic aeration for enhancing cold-water fish production. Under these conditions, trout which would normally be excluded from the hypolimnion, may feed on the benthic community recolonizing the aerated hypolimnion (Fast 1971) or make occasional forays through the anoxic metalimnion into the productive epilimnion (Serns 1976; Garrell et al. 1978).

Undersized equipment is a problem in hypolimnetic aeration and reflects the difficulties associated with correctly designing aerators and predicting hypolimnetic oxygen consumption during aeration (Lorenzen and Fast 1977). Taggart and McQueen (1982) recommend equivalent cross-sectional areas in riser and return manifold tubes; however, Taggart's (1984) return tube area was only 1/8 to 1/2 the riser tube area. Ashley (1984) recently proposed an empirical sizing formula for hypolimnetic aerators which should reduce this problem.

The design of Taggart's (1984) experiment was not well suited to studying zooplankton depth distribution. Hypolimnetic aeration is a whole-lake perturbation, and assessment of its effects requires appropriate comparison between control and treatment conditions, e.g. before and after, split-lake, side by side lakes, or in-lake controls. Taggart's (1984) experiment involved two treatment years (1978 and 1979) and no control data. The recent history of Tory Lake was confounded by 2 yr of destratification (1975 and 1976; Ellis and Tait 1981) which could effect zooplankton species composition and distribution (Fast 1971; Lackey 1973). In addition, in the first treatment year (1978) aerator leakage partially destratified the lake and during the second treatment year (1979) external nutrient loading increased 4.6-fold from 1978 (Taggart and McQueen 1981).

A frequent statement throughout Taggart's (1984) paper was that an "anoxic and toxic metalimnion" imposed a migration barrier on the zooplankton community. However, no data are given to specify lethal concentrations of oxygen or hydrogen sulfide, and only one 24-hr sampling period (July 4–5, 1979) was used to detect vertical migration in the Tory Lake zooplankton community. Burns and Mitchell (1980) suggested that zooplankton may migrate vertically through an anoxic metalimnion to reach an oxygenated hypolimnion.

In summary, I suggest that experimental design and equipment problems invalidated the main conclusions presented by Taggart (1984), and that an anoxic metalimnion may not preclude the development of epi- and hypo-limnetic zooplankton populations or reduce the effectiveness of hypolimnetic aeration for restoring cold-water fish production — Ken Ashley, *Ministry of Environment, Fish and Wildlife Branch, Fisheries Research Section, 2204 Main Mall, University of British Columbia, Vancouver, B.C. V6T 1W5.* *(J7877a)*

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Reply with Explanations and Additional Evidence

Ashley (1984) has levelled several criticisms against the experimental design and conclusions presented in Taggart (1984) which I believe derive in part from a superficial reading of the paper, some misconceptions, and an uncritical interpretation of other works on hypolimnetic aeration. Before responding in detail to each of Ashley's specific criticisms I wish to make clear that nowhere did I imply that an anoxic, H_2S-rich metalimnion would preclude the development of epilimnetic zooplankton populations, nor did I imply that hypolimnetic aeration *in general* is not effective in establishing suitable conditions for cold-water fish. I contended only that suitable biological conditions for cold-water fish production may be *limited* by the presence of an anoxic and H_2S-rich metalimnion. This conclusion was clearly indicated as tentative by the title of the paper. The paper was also meant to serve as a warning to researchers and lake managers that trophic, chemical, and thermal structure of their lakes should be considered carefully before managerial and research commitments to hypolimnetic aeration programmes are made — commitments that may prove to be costly and unrewarding.

It should also be emphasized that when the Tory Lake hypolimnetic aeration programme was implemented in 1978, this treatment was gaining acceptance as an ideal technique for restoring cold-water fish production in normally dimictic but oxygen-deficient lakes. Several fish stocking experiments were qualitatively successful, but no reports on zooplankton responses to hypolimnetic aeration had been published. A need for such information was later articulated by Fast (1979).

I turn now to Ashley's specific criticisms and deal first with his suggestion that aeration had little effect on hypolimnetic oxygen concentration. The facts are as follows: (1) During 1973–74, and early 1975 (prior to any type of aeration), Tory Lake had an anoxic meta- and hypo-limnion when stratified (see references in Taggart 1984). (2) Hypolimnetic aeration stripped H_2S from the hypolimnion and prevented hypolimnetic anoxia for two consecutive summers, but the anoxic, H_2S-rich metalimnion was unaffected. (3) Aeration of Tory Lake ceased in mid-July 1980, and monitoring since then shows that the lake has reverted to meta- and hypo-limnetic anoxia, and H_2S-rich conditions when stratified (D. J. McQueen, York University, Toronto, Ont., pers. comm. and unpubl. data). These facts are inconsistent with Ashley's assertion that aeration had little effect on hypolimnetic $[O_2]$ in 1978–79.

Ashley (1984) cites Overholtz (1977) and Ashley (1983b) to support his claim that a suitable cold-water habitat for zooplankton and fish can be created by hypolimnetic aeration. I do not question this, but it should be made clear that no anoxic, H_2S-rich metalimnion formed in either of the lakes referred to in those papers. Ashley further cites Serns (1976) and Garrell et al. (1978) as evidence that trout "make occasional forays through the *an*oxic metalimnion" (my italics). In neither of the studies cited was the metalimnion anoxic (0.5–0.7 mg O_2/L in Larson Lake, Serns 1976; 0.2 mg O_2/L in Lake Waccabuc, Fast et al. 1975), and more important, there was no report of H_2S in the metalimnion of either lake during aeration. The evidence for fish movement through the hypoxic metalimnion provided by Serns (1976) is convincing, though based on a sample of only 10 marked fish. That provided by Garrell et al. (1978), however, was based not on distributional observations, but rather on the analysis of the stomach contents of nine fish collected 2 yr after aeration and stocking began, and no data on the condition of the metalimnion at the time of capture were reported.

Trapping of fathead minnows (*Pimephales promelas*) on 29 October 1978, in Tory Lake (at 1-m intervals from surface to 5 m), when the lake was destratified and $[O_2]$ was slightly less than 4 mg/L, resulted in a total catch of 1532 vigorous individuals which were uniformly distributed through the water column (Taggart 1980). Fish trapping was conducted a second time to a depth of 8.5 m on 4 July 1979 when the lake was well stratified and $[O_2]$ was 4.3 mg/L in the hypolimnion. A total of 655 individuals were captured. None were captured in the hypolimnion, and although 191 were captured at 2 m, and 2 individuals at 3.5 m, the combined mortality was 98.4% at the time of trap retrieval (7 h after set). Mortality at 0.5 and 1.0 m was 0.0%. These observations indicate that the dead fish were asphyxiated, and that although capable of penetrating the metalimnion, there is no evidence that they passed through it. Magnuson and Karlen (1970) have observed that several freshwater fish species occasionally sound into an anoxic layer containing H_2S, but note that the behavior is most pronounced shortly before death occurs, and caution that the behavior may have been an artifact of the experiment.

Ashley's (1984) concern for aerator design is justified, as aerator design can have critical effects on water flow and oxygen transfer efficiency, but he has misinterpreted the design model of Taggart and McQueen (1982). It is true that the return manifold in the Tory Lake aerator was undersized during 1978. In 1979 the manifold area was increased fourfold (Taggart and McQueen 1981) and was easily capable of handling maximum water flow from the riser, indicating not that the return manifold was undersized, but rather that the riser was oversized. In fact, the design model indicated that the radius of the riser was at least 1.5 times greater than required (Taggart and McQueen 1982, table 1).

Ashley's (1984) requirement for "control" and treatment comparisons in a whole lake manipulation broaches the subject of pseudoreplication (Hurlbert 1984). The Tory Lake aeration programme can be classified as simple or temporal pseudoreplication, which is "neither surprising nor bad" when one is manipulating a whole lake, when a rough estimate of the treatment effect is anticipated, and when the cost of replication is financially crippling (Hurlbert 1984). Furthermore, the conclusion and accompanying warning in Taggart (1984) were not given "the unmerited veneer of rigor by the erroneous application of inferential statistics" (Hurlbert 1984).

Destratification aeration of Tory Lake during 1975–76 (Ellis and Tait 1981) may well have affected zooplankton species composition as Ashley suggests, and it certainly did affect depth distribution (see Taggart 1984). What should be recognized however, is that during periods of hypolimnetic aeration (when $[O_2]$ in the hypolimnion exceeded 3 and 4 mg/L) only rotifers were found there. Ellis and Tait (1981), on the other hand, showed that at equivalent and lower $[O_2]$, but in the absence of an anoxic H_2S-rich zone, zooplankton significantly increased their depth distribution to 8 m.

Ashley has also pointed out the fact that Tory Lake partially destratified early in 1978 and increased external nutrient loading

was experienced in 1979. These were unfortunate and unforseeable events. However, the short period of destratification served only to increase the depth distribution of zooplankton to the hypolimnion (Taggart 1984, fig. 2, 3, 5). Moreover, while oxygen conditions in the hypolimnion were improved by aeration following restratification, none of the "stocked" species persisted. The aerator was capable of handling the increased nutrient loading when compared with 1978 (Taggart and McQueen 1981), and therefore, I see no reason why increased loading per se should affect the depth distribution of zooplankton. (In retrospect it is interesting to note that the establishment of the only hypolimnetic zooplankton population occurred in the year of increased loading.)

Ashley's criticism of my failure to specify lethal concentrations of O_2 or H_2S is well founded. However, aquatic invertebrates are known to be variable in their ability to tolerate low oxygen conditions (Davis 1975), and there is no general consensus on critical levels. This fact is illustrated by the disagreement between referees of the original manuscript, one of whom argued that most zooplankters are tolerant of low $[O_2]$, while the other argued that most would avoid a concentration of 4 mg/L. When preparing this reply a search was made of four data bases, one extending back to 1967. Several studies from field sampling programmes were identified that confirmed that most, but not all, zooplankton species will respond to and avoid anoxic, H_2S-rich strata (Heberger and Reynolds 1977; Boyd and Smith 1980; Judkins 1980; Chapman et al. 1981; Thain et al. 1981; Hamner et al. 1982; Caumette et al. 1983; see also references in Taggart 1984). Surprisingly, there were no experimental studies on toxicity or tolerance levels of zooplankton to H_2S.

Tolerance and toxicity levels are well documented for fishes, and many species are sensitive to low $[O_2]$, and can tolerate reduced levels for a short period (Davis 1975). H_2S is toxic at levels well below 1 mg/L, and becomes increasingly so as $[O_2]$ decreases and pH and/or temperature increase (Bonn and Follis 1967; Adelman and Smith 1970, 1972; Smith et al. 1976; Broderius et al. 1977). Acclimation to low $[O_2]$ does not appear to decrease H_2S toxicity (Adelman and Smith 1972). Smith et al. (1976) suggested that regular monitoring in the field may not be able to detect the low levels of H_2S known to have toxic effects and therefore "any detectable concentration in the field should be considered detrimental to fish production." This advice is well founded, as inversions or wind-generated mixing of H_2S zones may result in high mortality of fish and zooplankton (Fedorenko et al. 1979; Infante et al. 1979).

Ashley's (1984) criticism of only one 24-h sampling period for detecting vertical migration would be valid had I set out to investigate diel migration per se, where cues, feeding strategies, energetics, predator avoidance, etc., are of prime importance. However, in Tory Lake I was interested only in determining how deep the zooplankton would go and if they penetrated the metalimnion. As virtually all the species recorded in Tory Lake are known to display typical downward migration during the early morning, it was not unreasonable (see for example Thain et al. 1981) to assume that they would be at, or very near, their deepest between 11:00 and 14:00 when the regular sampling was performed. The diel sampling was conducted solely to determine if there was *any* evidence of reverse migration (downward during the evening or night). As there was not the slightest evidence of this rare behavior, even when $[O_2]$ in the hypolimnion was very near the highest observed during the summer, no further diel sampling was thought necessary.

The working hypothesis during the Tory Lake study was that zooplankton populations would establish themselves in the hypolimnion if chemical conditions there were improved by aeration. Conditions were improved (Taggart 1980; Taggart and McQueen 1981), but the expected zooplankton response was not apparent during the 2 yr of treatment. All evidence indicates that the lack of response was due to the anoxic, H_2S-rich metalimnion. The conditional conclusion presented in Taggart (1984) was negative with respect to what is expected to result from hypolimnetic aeration, but only when an anoxic H_2S-rich metalimnion is present. To this I add the following: "if a testable hypothesis produces negative results, with some degree of uncertainty, then that hypothesis is preferable to an untestable one that fits more closely a current or popular paradigm" (Price et al. 1984), particularly if it is one that has never been tested but is becoming accepted and ingrained in the literature.

Indeed, the lack of appreciable response by zooplankton to hypolimnetic aeration may be an even more general phenomenon than I have previously suggested (Taggart 1984). Ashley's own work indicates that in the absence of an anoxic, H_2S-rich metalimnion, and in the presence of a hypolimnion where "Oxygen concentrations were significantly higher" (Ashley 1983a, p. 1348), "zooplankton did not respond as expected to the experimental treatment" (Ashley 1983b, p. 38). — Christopher T. Taggart, *Department of Biology, McGill University, 1205 Avenue Docteur Penfield, Montreal, Que. H3A 1B1.*

(*J7877b*)

Acknowledgments

I thank Dr. D. J. McQueen for making unpublished data available and S. F. McRae for assistance.

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ANNOUNCEMENTS/AVIS

International Conference on Arctic Water Pollution Research: Applications of Science and Technology, 1985

The International Conference on Arctic Water Pollution Research will be held in Yellowknife, Northwest Territories, Canada, from April 28 to May 1, 1985. It is being organized under the aegis of the International Association on Water Pollution Research and Control.

The purpose of the conference is to understand and assess the nature of water pollution at low temperatures and in the presence of ice. The consequence and the control of arctic pollution is of great importance with the ever increasing industrial and community development in the arctic area.

The major topics of the conference are as follows: Sources, Movement, and Accumulation of Pollutants in the Arctic Environment; Interactions Between Pollutants and the Abiotic Arctic Environment; Effects on Arctic Biological Systems; Pollution Prevention and Control Under Arctic Conditions; Management, Information for Decisions.

The program will include invited and contributed papers.

To receive the current circular which contains additional information on the conference including the field trips, please contact:

K. Charbonneau
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National Research Council of Canada
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Conférence internationale de la recherche sur la pollution des eaux de l'arctique : applications des sciences et de la technologie, 1985

La Conférence internationale de la recherche sur la pollution des eaux de l'Arctique aura lieu à Yellowknife (Territoires du Nord-Ouest), Canada, du 28 avril au 1 mai 1985. La conférence est organisée sous l'égide de l'Association internationale pour la recherche sur la pollution de l'eau et sa maîtrise.

Le but de la conférence est de pouvoir comprendre et d'évaluer la nature de la pollution de l'eau dans les régions de basses températures et englacées. Les conséquences et la maîtrise de la pollution en fonction du milieu arctique sont très importantes en vue de l'expansion des activités industrielles et des agglomérations dans les régions arctiques.

Les principaux sujets de la conférence sont les suivants : Sources, migration et accumulation des polluants en milieu arctique ; Interactions entre les polluants et le milieu abiotique arctique ; Effets sur les systèmes biologiques arctiques ; Prévention et maîtrise de la pollution en milieu arctique ; Gestion, information et prise de décision.

Des mémoires invités et soumis seront inclus au programme.

Pour recevoir la première circulaire qui comprend de plus amples renseignements sur la conférence et sur les excursions, veuillez vous addresser à :

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Canadian Waters: The State of the Resource

Toronto, May 1985

A symposium on this timely topic will be held May 26–29, 1985, at the Royal York Hotel, Toronto. The Rawson Academy of Aquatic Science, a nonprofit Canadian organization made up of aquatic resource-oriented scientists, educators, and managers from across Canada, is hosting this national review of aquatic resources, their quantity, quality, and distribution in relation to present and projected demand.

Twenty theme papers will be presented on diverse aquatic-related topics, and contributed scientific papers will be presented at concurrent sessions at the symposium. Invited papers reviewing significant scientific, technical, and policy information will be edited and published by the Academy.

Enquiries regarding registration, exhibit, and display space, student assistance, and spouse's program should be directed to the Symposium Co-ordinator, The Rawson Academy of Aquatic Science, No. 200, 601-17 Avenue S.W., Calgary, Alta. T2S 0B3. Telephone: (403) 228-0407.

Les eaux canadiennes : situation de nos ressources

Toronto, mai 1985

Un colloque sur ce sujet d'actualité aura lieu du 26 au 29 mai 1985 à l'hôtel Royal York de Toronto. L'Académie Rawson des sciences aquatiques, un organisme canadien à but non lucratif formé de scientifiques, d'éducateurs et de gestionnaires de tout le Canada s'intéressant aux ressources aquatiques, parraine cet examen national des ressources aquatiques en ce qui concerne leur quantité, leur qualité et leur répartition par rapport à la demande présente et prévue.

Vingt mémoires seront présentés sur divers sujets liés au ressources aquatiques, ainsi que d'autres documents, lors de séances parallèles au cours du colloque. Les mémoires sollicités portant sur des aspects scientifiques, techniques et politiques seront édités et publiés par l'Académie.

Les demandes de renseignements concernant l'inscription, la présentation de matériel, l'aide d'étudiants et le programme pour les conjoints doivent être adressées directement au coordonnateur du colloque, The Rawson Academy of Aquatic Science, No. 200, 601-17 Avenue S.W., Calgary (Alta.) T2S 0B3. Téléphone : (403) 228-0407.

COMING NEXT MONTH/À PARAÎTRE LE MOIS PROCHAIN

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Fleet dynamics and individual variation: why some people catch more fish than others **R. Hilborn**

Growth of the euphausiids *Thysanoessa inermis*, *Thysanoessa raschii*, and *Meganyctiphanes norvegica* in a subarctic fjord, North Norway **S. Falk-Petersen**

Accumulation of copper and zinc in the yellow water lily, *Nuphar variegatum*: relationships to metal partitioning in the adjacent lake sediments **P. G. C. Campbell, A. Tessier, M. Bisson, and R. Bougie**

Conversion of blade length increments into biomass production estimates in *Laminaria longicruris* **L. Gendron**

Chloroform–methanol extraction of chlorophyll *a* **L. W. Wood**

Generalizing fisheries models: an extension of the Schaefer analysis **E. Tsoa, W. E. Schrank, and N. Roy**

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Assessing significance of physiological differences among three esocids with a bioenergetics model **M. S. Bevelhimer, R. A. Stein, and R. F. Carline**

Dissipation of permethrin in limnocorrals **K. R. Solomon, J. Y. Yoo, D. Lean, N. K. Kaushik, K. E. Day, and G. L. Stephenson**

Impact of permethrin on zooplankton communities using limnocorrals **N. K. Kaushik, G. L. Stephenson, K. R. Solomon, and K. E. Day**

Zinc–phosphorus interactions and variation in zinc accumulation during growth of *Chlamydomonas variabilis* (Chlorophyceae) in batch culture **S. S. Bates, A. Tessier, P. G. C. Campbell, and M. Létourneau**

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Feeding ecology of the sauger (*Stizostedion canadense*) in a large river **D. H. Wahl and L. A. Nielsen**

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Responses of benthic macroinvertebrate species to manipulation of interstitial detritus in Cornation Creek, British Columbia **J. M. Culp and R. W. Davies**

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Journal canadien des sciences halieutiques et aquatiques

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CJFSDX41(12) 1722–1862 (1984)
ISSN 0706-652X
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Ministre des Approvisionnements et Services Canada 1984

Subscription rates/Abonnements
Canada $66.65
Other countries/Autres pays $80.00